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A TAXONOMIC CONSPECTUS OF PHRYMACEAE: A NARROWED CIRCUMSCRIPTION FOR *MIMULUS*, NEW AND RESURRECTED GENERA, AND NEW NAMES AND COMBINATIONS

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ABSTRACT

A revised taxonomic classification of Phrymaceae down to species level is presented, based on molecular-phylogenetic and morpho-taxonomic studies, setting a framework for ongoing work. In the concept adopted, the family includes 188 species divided into 13 genera. All species as currently understood are listed and assigned to genera and sections which in several cases have new circumscriptions requiring many new combinations. Four main clades are recognized. Clade A. An Asian-African-Australasian-centered clade of 7 genera: *Mimulus* L. sensu stricto (7 species) of North America, Asia to Africa, and Australasia is sister to an Australian-centered group that comprises *Elacholoma* (2 species), *Glossostigma* (5 species), *Microcarpaea* (2 species), *Peplidium* (4 species), *Uvedalia* (2 species) and a new monotypic genus *Thyridia*, described here. The remaining three clades are largely American, with a few east Asian species. Clade B. Monotypic *Phryma* forms its own clade. Clade C. *Hemichaena* (5 species), *Mimetanthe* (1 species), and *Diplacus* (46 species). Clade D. *Leucocarpus* (1 species) and *Erythranthe* (111 species). A new infrageneric classification is constructed for the two largest genera — *Diplacus* with six sections, and *Erythranthe* with 12. The sessile to subsessile flowers and parietal placentation of *Diplacus* distinguish it from *Erythranthe*, which has long-pedicellate flowers and axile placentation. Descriptions are provided for all inframilial, generic, and infrageneric taxa and full synonymies enable a comparison with previous classifications.

KEY WORDS: *Mimulus*, *Uvedalia*, *Microcarpaea*, *Elacholoma*, *Peplidium*, *Glossostigma*, *Thyridia*, *Diplacus*, *Erythranthe*, *Mimetanthe*, *Hemichaena*, *Leucocarpus*, *Phryma*, Phrymaceae, Mazaceae, sections, typification

TAXONOMIC SUMMARY

Mimulus L. sensu stricto includes only two primarily eastern North American species, *M. ringens* L. (the type) and *M. alatus* Sol. ex Ait., and five species from Asia and the Southern Hemisphere: *M. gracilis* R. Br. (here confined to Australia), *M. strictus* Benth. (resurrected for Old World plants previously identified mostly as *M. gracilis*), *M. madagascariensis* Benth., *M. aquatilis* A.R. Bean, and *M. orbicularis* Wall. ex Benth. The sister clade is Australian-centered, including the long-recognized genera *Elacholoma* F.Muell. & Tate (2 named species, one formerly *M. prostratus* Benth.), *Glossostigma* Wight & Arn. (5 species), *Microcarpaea* R. Br. (2 species), *Peplidium* Delile (4 species), *Uvedalia* R. Br. (2 species, removed from traditional *Mimulus*), and monotypic **Thyridia** W.R. Barker & Beardsley, gen. nov. (type *T. repens*, formerly *Mimulus repens* R. Br.). Monotypic *Phryma* L. forms its own clade. The remaining two clades are largely American, with a few east Asian species: one includes *Hemichaena* Benth. (5 species), *Mimetanthe* Greene (1 species), and *Diplacus* Nutt. (46 species); the other includes *Leucocarpus* D. Don (1 species), and *Erythranthe* Spach (111 named species). *Diplacus* includes species segregated by A.L. Grant as subg. *Schizoplacus* and by Nuttall, Bentham, Greene, and others as the genera *Diplacus* and *Eunanus*. *Mimetanthe* was recognized as a monotypic section by Bentham and Asa Gray and then at generic rank by Greene in 1886. *Erythranthe* comprises species mostly segregated by A.L. Grant as subg. *Synplacus*, including the group of species closely related to the type, *E. cardinalis* (sect. *Erythranthe*). In a sister relationship to *Erythranthe* is the monotypic genus *Leucocarpus*; sister to *Diplacus* is *Mimetanthe*, and sister to that pair is *Hemichaena*. Sister to the combined *Hemichaena-Mimetanthe-Diplacus* and *Leucocarpus-Erythranthe* clade is *Phryma*. *Diplacus* is divided into 6 sections (types in parenthesis): (1) sect. **Erimimimulus** G.L. Nesom & N.S. Fraga, sect. nov. (*D. parryi*), (2) sect. **Eunanus** (Benth.) G.L. Nesom & N.S. Fraga, comb. nov. (*D. nanus*), (3) sect. **Pseudoenoe** (A.L. Grant) G.L. Nesom & N.S. Fraga, comb. nov. (*D. pictus*), (4) sect. **Oenoe** (A. Gray) G.L. Nesom & N.S. Fraga, comb. nov. (*D. tricolor*), (5) sect. **Cleisanthus** (J.T. Howell) G.L. Nesom & N.S. Fraga, comb. nov. (*D. douglasii*), and (6) sect. *Diplacus* (*D. aurantiacus*). *Erythranthe* is divided into 12 sections (types in parenthesis): *Erythranthe* is divided into 12 sections (types in parenthesis): (1) sect. **Achlyopitheca** G.L. Nesom & N.S. Fraga, sect. nov. (*E. inconspicua*), (2) sect. **Paradantha** (A.L. Grant) G.L. Nesom & N.S. Fraga, comb. nov. (*E. rubella*), (3) sect. **Monantha** G.L. Nesom & N.S. Fraga, sect. nov. (*E. primuloides*), (4) sect. **Monimanthe** (Pennell) G.L. Nesom & N.S. Fraga, comb. nov. (*E. breweri*), (5) sect. *Erythranthe* (*E. cardinalis*), (6) sect. **Alsinimimulus** G.L. Nesom & N.S. Fraga, sect. nov. (*E. alsinoides*), (7) sect. **Sinopitheca** G.L. Nesom & N.S. Fraga, sect. nov. (*E. sessilifolia*), (8) sect. **Simigemma** G.L. Nesom & N.S. Fraga, sect. nov. (*E. gemmipara*), (9) sect. **Mimulasia** G.L. Nesom & N.S. Fraga, sect. nov. (*E. tenella*), (10) sect. **Mimulosma** G.L. Nesom & N.S. Fraga, sect. nov. (*E. moschata*), (11) sect. **Exigua** G.L. Nesom & N.S. Fraga, sect. nov. (*E. exigua*), and (12) sect. **Simiola** (Greene) G.L. Nesom & N.S. Fraga, comb. nov. (*E. guttata*). Lectotypes are designated for *Mimulus* subg. *Synplacus*, *Erythranthe* sect. *Paradantha*, *Erythranthe* sect. *Simiola*, and four unranked but validly published species groups named by Bentham: § *Erecti*, § *Prostrati*, § *Speciosi*, and § *Teneri*.

Recent molecular-phylogenetic studies have greatly altered concepts of families of the traditional Scrophulariaceae (e.g., Olmstead and Reeves 1995; Oxelman et al. 2005; Tank et al. 2006; Beardsley & Olmstead 2002; Beardsley et al. 2004; Beardsley & Barker 2005). Surprisingly, *Mimulus* L. sensu lato is indicated to be closely related to the monotypic genus *Phryma* L., which usually has been placed in Verbenaceae or Lamiaceae (e.g., Whipple 1972). Also closely related to *Phryma* and *Mimulus* are the American genera *Hemichaena* Benth., *Leucocarpus* D. Don, and a group of small Australian-centered genera: *Elacholoma* F. Muell. & Tate, *Glossostigma* Wight & Arn., *Microcarpaea* R. Br. and *Peplidium* Delile. The correct family name for this group of 188

species is Phrymaceae (see below). Recent phylogenetic studies have centered on Phrymaceae and its close relatives (Beardsley & Olmstead 2002; Beardsley et al. 2004; Beardsley & Barker 2005).

The study by Beardsley et al. (2004) included about 105 species that are maintained in the current account and provides a useful guide toward understanding the taxonomy and systematics of American *Mimulus* sensu lato. It strongly supports the hypothesis that a broadly conceived *Mimulus* is not monophyletic. Beardsley and Barker (2005) concentrated on providing a phylogenetic hypothesis for the Australian species, confirming Barker's (1982, 1986) view that the highly modified semiaquatic Australian-centered genera had close relationships with *Mimulus* in the Mimulinae (Wettstein 1891) or Mimuleae (Bentham & Hooker 1876) of the traditional Scrophulariaceae. To that time these genera had been placed with other genera of small aquatics or semi-aquatics in the Gratioleae (Bentham & Hooker 1876) or in subtrib. Limosellinae of the Gratioleae (Wettstein 1891); they were not listed close to *Mimulus, Phryma* and *Mazus* Lour., reflecting their obscure relationships. More recently, Fischer (2004) resurrected Trib. Microcarpaeeae Miq. (as "Microcarpeae") for such small, often aquatic or semi-aquatic plant groups of "uncertain placement in Digitaloideae" (as "Digitalioideae").

The genera *Mazus* Lour. (ca. 25-30 species) and *Lancea* J.D. Hook. & T. Thomson (2 species) were weakly supported as forming a clade sister to *Mimulus* sensu lato in Beardsley and Olmstead (2002) and were tentatively included in the Phrymaceae at the rank of subfamily ("Mazoideae" ined.). Later studies have placed these two genera apart from Phrymaceae sensu stricto (Oxelman et al. 2005; Albach et al. 2009; Schäferhoff et al. 2010) and essentially agreed that the family is most appropriately constituted as treated here. Mazaceae, as now formally described (Reveal 2011), is available to include both *Mazus* and *Lancea*. Plants of the latter two genera, however, have bilamellate, sensitive stigmas like the Phrymaceae and Reveal's brief description of Mazaceae does not distinguish it morphologically from Phrymaceae. We are unable to find apomorphies to distinguish Phrymaceae, but it seems likely that further morphological study will corroborate the distinction between Mazaceae and Phrymaceae. The broader phylogenetic patterns underlying the taxonomy of the present treatment are derived primarily from molecular analyses, as also apparently with Reveal's implicit assumption.

Phylogenetic relationships within Phrymaceae

Molecular-phylogenetic studies in the Phrymaceae over the last decade, notably by Beardsley and Olmstead (2002), Beardsley et al. (2004), and Beardsley and Barker (2005), are summarized in a phylogeny of the family shown in Figure 1. This diagram shows that species of Phrymaceae are divided into four major clades, denoted as Clade A, the "Australasian-Old World lineage," Clade B, the monotypic *Phryma* (its phylogenetic position not well-resolved), and Clades C and D, constituting an "American-Asian lineage." The phylogenetic diagram is based on a subset of species in most taxa. To complete a comprehensive taxonomic account of the family, additional taxa have been interpolated based on morphological features. We note under the genera and infrageneric taxa where there are doubts about traditional infrageneric placement of species.

The "Australasian-Old World lineage" includes 23 named species (with about 17 yet to be named; Table 1) from Australia, New Zealand, southeastern Asia, eastern North America, India, Madagascar, and South Africa. In the earliest divergence within this lineage, *Mimulus* sensu stricto, based on DNA sequences from the type *M. ringens*, *M. alatus* and *M. gracilis* is sister to a lineage that includes Australian-centered genera. The six genera are these: *Elacholoma*, *Glossostigma*, *Microcarpaea*, and *Peplidium*, which have long been recognized, and two groups that have been been previously placed in *Mimulus* in its traditionally broad circumscription — one of these groups is recognized here by the resurrected generic name *Uvedalia* R. Br., the other in the new genus *Thyridia*.

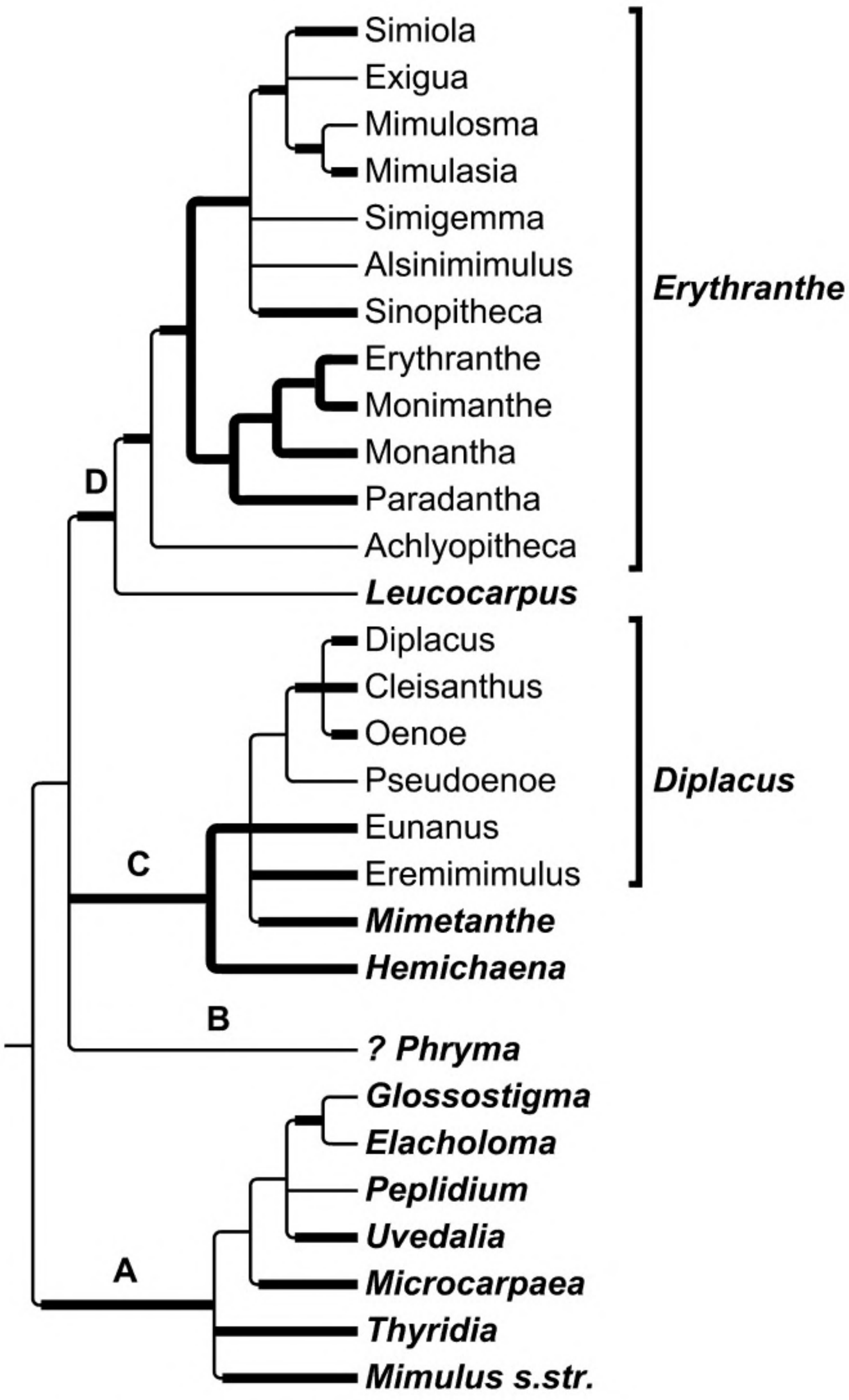

Figure 1. Summary/hypothesis of phylogenetic relationships of Phrymaceae essentially as defined by Oxelman et al (2005), primarily from data from Beardsley et al. (2004) and Beardsley and Barker (2005), showing the generic and infrageneric classification adopted here. Nodes with less than 50% bootstrap support are collapsed. *Thyridia* has a 59% bootstrap value but that node was collapsed in the strict consensus tree, so it is collapsed here. Bolded branches indicate greater than 80% bootstrap support. The position of *Phryma* is based on a maximum likelihood tree inferred using combined data (Beardsley & Olmstead 2002); alternatively, the ML tree resulting from the analysis of nrDNA ITS and ETS sequence data places *Phryma* at the base of the tree and sister to the remaining Phrymaceae. A is the Australasian-Old World lineage, B-C-D the American-Asian lineage. Genera are in bold italic and sections in normal font. Sectional names in *Diplacus* and *Erythranthe* include those newly proposed here.

The "American-Asian lineage" includes 165 species (Table 1) from North, Central, and South America, and southeast Asia. This lineage includes two genera from Mexico and Central America — (1) *Hemichaena*, which is sister to the monotypic North American *Mimetanthe* and a resurrected North American genus *Diplacus*, and (2) *Leucocarpus*, which is sister to a group of North American and Asian species here placed in a resurrected genus *Erythranthe*. These clades, designated Clade C and Clade D, respectively in Figure 1, are interpretated as indicating two distinct radiations of *Mimulus* sensu lato in western North America..

Phryma is divided between eastern North America and eastern Asia. Molecular data provide two alternative relationships of the genus to the two major clades. A maximum likelihood tree inferred using combined data (Beardsley & Olmstead 2002) places it as sister to the "American-Asian lineage." Alternatively, the ML tree resulting from the analysis of nrDNA ITS and ETS sequence data positions *Phryma* as sister to the remaining genera of Phrymaceae. In view of its morphological disparity, the latter position seems most probable for *Phryma*, which could ultimately return to its status as a monotypic family.

Taxonomic options

The phylogenetic placement of *Mimulus* sensu stricto, separate from other species included in *Mimulus* in North America, Central America, South America, and Southeast Asia, leads to consideration of how the group might be best treated taxonomically and nomenclaturally to provide an informative and stable taxonomic framework. Four general options are outlined below, accompanied by our evaluation of each. Relative merits of taxonomic approaches to the same problem also have been discussed by Beardsley and Olmstead (2002) and Beardsley and Barker (2005).

1. A phenetic, polyphyletic or paraphyletic approach, enabling retention of current generic circumscriptions with minimal name changes for species.

Maintain the taxonomic and nomenclatural status quo, recognizing *Mimulus* either as polyphyletic following the Grant's (1924) broad circumscription of the genus, adopted also by later authors (represented by *Mimulus* sensu stricto, *Diplacus* and *Erythranthe* in Fig. 1), or as biphyletic (if *Leucocarpus* and *Hemichaena* are incorporated within *Mimulus*).

We prefer to recognize monophyletic taxa, especially because the clades are strongly supported by molecular data and most are morphologically distinctive. Where morphological differences appear to be minimal (see notes below on *Mimulus* s. str. vs. *Erythranthe*), we suspect that further study will provide better discrimination.

2. A phyletic approach with minimal species name changes, minimally informative at generic level.

Treat Phrymaceae as comprising the single genus *Mimulus* L. *Uvedalia*, *Thyridia*, *Elacholoma* partly, *Hemichaena*, and *Leucocarpus* already have names in *Mimulus*. This would require fewer than 13 new combinations for species in Australian-centered genera and the one in *Phryma*.

Maximally enlarging *Mimulus* results in the loss of much useful information in the taxonomic hierarchy that recognizes the Australian-centered genera as well as *Phryma*, *Leucocarpus*, *Hemichaena*, *Diplacus*, *Mimetanthe*, and *Erythranthe*, each of which has apparent apomorphic features that justify treatment at generic rank.

3. A phyletic approach, highly informative at generic level, with minimal species name changes through conservation of *Mimulus* L. with a new type.

Retaining *Mimulus* for a large number of species under this scenario would require conserving the name *Mimulus* L. with a different type species chosen from one of the two American

generic-level groups *Diplacus* or *Erythranthe*. This would enable *Phryma* and the Australian-centered genera to be maintained at generic level. A new name (*Cynorrhynchium*) would apply to the species separated here as *Mimulus* sensu stricto.

The least nomenclaturally disruptive course under this scenario is to maintain the 164 species (excluding *Phryma*) of North America, Central America, South America, and Asia in a single genus with the name *Mimulus*, though it would require combining five genera in the American-Asian lineage recognized in the current account (Fig. 1) into *Mimulus*, requiring the exclusion of *Leucocarpus*, *Mimetanthe* and *Hemichaena*. This option was one suggested by Beardsley and Barker (2005) and was the rationale for formally bringing *Leucocarpus* and *Hemichaena* into *Mimulus* (Nesom 2011a). Grant (1924) already had included one of the *Hemichaena* species within *Mimulus* (as sect. *Tropanthus*).

A second alternative under this approach would be to maintain *Leucocarpus*, *Mimetanthe*, and *Hemichaena*, as well as *Diplacus* and *Erythranthe*, as distinct genera. The name *Mimulus* L. would be maintained for the larger group, *Erythranthe*, by conserving it with a new type chosen from among those 111 species, where the few species of *Mimulus* in the traditional sense that are significant in horticulture and genetic studies belong, as discussed below. About 35 further name changes would be required for recognition of *Diplacus* as a distinct genus, but this would need to happen whether or not the name *Mimulus* is conserved.

This option requires use of a different name for the group of eight species currently treated as *Mimulus* L, including *M. ringens* L. and *M. alatus* Ait., widespread species mostly in the eastern USA, as well as for others of Asia and the Southern Hemisphere. The option that prompts the fewest name changes at species rank submerges *Hemichaena* and *Leucocarpus*, both of which are justifiably treated as distinct genera, as are *Diplacus* and *Erythranthe*. Alternatively, by recognizing all American genera in the current account but conserving *Mimulus* with a new type chosen from within *Erythranthe*, about 43 name changes still would be required for recognition of *Diplacus* and to accomodate the species formerly of *Mimulus* sensu stricto.

4. A phyletic approach highly informative at generic level, retaining *Mimulus* with its Linnaean type, requiring many name changes for species of *Diplacus* and *Erythranthe*.

Treat *Mimulus* sensu stricto as seven species, maintaining the currently recognized Australian-centered genera (adding the new monotypic genus *Thyridia* and resurrected *Uvedalia*) and the Asian-American *Phryma*, *Leucocarpus*, *Mimetanthe* and *Hemichaena*. Under this option the remainder of the two American clades would be segregated at generic rank. The resurrected segregates (*Erythranthe* and *Diplacus*) are two credible genera, immediately discernable by a conspicuous feature of relative pedicel length (long-pedicellate vs. short-pedicellate flowers), and they have different placentation and modes of capsule dehiscence. Species of *Hemichaena*, *Mimetanthe*, *Leucocarpus*, and some species of the two resurrected genera already have species names in those genera, reflecting traditions of separation from *Mimulus*. About 136 new combinations are needed for American-Asian species; a much smaller set of combinations is required in Australasia.

This is the option followed here. It maximally incorporates and reflects phylogenetic information now available from recent molecular studies, particularly the recognition of two distinct major radiations in western North America and the relationship of the eastern USA species to the Asian-African-Australasian lineage. This option is essentially similar to the second alternative of option 3, but it requires more name changes (adding those necessary for *Erythranthe*). While requiring the greatest number of name changes, option 4 is based on simple priority and normal typification. It avoids a need to invoke conservation under the ICN,

thus retaining the original Linnaean genus and species (*Mimulus* L., *Mimulus ringens* L.) in their original conception, without the necessity of making new combinations in *Cynorrhynchium* J. Mitchell for *M. ringens* and others of *Mimulus* L. sensu stricto described by Bentham, Aiton, and Robert Brown. It also avoids the peculiar situation of recognizing one of the major groups of western American species (*Diplacus*) by a segregate name while maintaining the other group (*Erythranthe*) as *Mimulus*. Not required is a wait of six years for a formal decision on conservation by the IBC.

In relation to our decision to maintain *Mimulus* as a small genus, we note that a recent proposal (O'Kane et al. 1999) to conserve the name *Lesquerella* (88 species) for the genus formed by the merger of *Lesquerella* with the older *Physaria* (22 species) was rejected (Brummitt 2000). *Eupatorium* has been reduced from a huge genus (ca. 800 species) to one of about 40 species (King & Robinson 1987), with a number of the segregates considerably larger than the remaining *Eupatorium* sensu stricto. On the other hand, names were recently conserved for *Centaurea* (Greuter et al. 2001; Brummitt 2004) and *Acacia* (Orchard & Maslin 2005; Brummitt 2004; Luckow et al. 2005; McNeill et al. 2011) — but these involved potential name changes in 5 and 10 times more species than is the case in the *Mimulus* example. Decisions on *Acacia* at two international congresses were made narrowly, and the controversy is not over, perhaps not even settled (Smith & Figueiredo 2011; Brummitt 2011; Turland 2011). Where endorsement is sought for changing long-established names primarily on the grounds of reduced number of nomenclatural changes, future IBC nomenclatural sessions may not be so much in agreement with the nomenclatural committee's recommendations.

Other rationale for conserving *Mimulus* with a new type is not so strong. While popular horticultural species known as *Mimulus* appear exclusively to belong to American-centered generic elements that do not include the generic type, they are relatively few in number. In *Erythranthe,* they include the subshrubby *E. cardinalis*, herbaceous *E. guttata*, and the South American *E. lutea* and *E. cuprea*, and in *Diplacus D. bigelovii* and the woody *D. aurantiacus* and *D. puniceus* of sect. *Diplacus*). Genetic studies have focused intensely on species of *Erythranthe*, but relatively few species are involved — *E. cardinalis* and *E. lewisii* of sect. *Erythranthe* and *E. guttata* and *E. nasuta* plus a few others of sect. *Simiola*.

Taxonomic comparisons and synonymy

Selected taxonomic works dealing at a family level or with the genus *Mimulus* are summarized in Table 1, but detailed comparison of classifications is set out in the synonymies and misapplications presented in the Appendix to the taxonomic treatment. Synonymies are confined to key publications for each group. Thompson (2005) gives a complete synonymy for *Diplacus*. Details of synonymy for much of *Erythranthe* are presented in studies published simultaneously with the present one (Nesom) and submitted (Fraga). Revisions are in progress in the Australasian-Old World lineage (Barker).

Summary of current classification compared with those of the past

Circumscription of some genera recognized in this study has been consistent for more than 150 years, namely *Microcarpaea*, *Peplidium*, *Glossostigma*, *Phryma*, *Mimetanthe*, and *Leucocarpus* (see Table 1). These long perceived distinctions, confirmed by molecular data, are maintained in our classification.

Mimulus previously has been defined with an alternatively narrow or broad circumscription, but it has consistently included *Mimulus* sensu stricto (in the sense adopted here) and the Australasian *Thyridia*, *Uvedalia*, and *Elacholoma prostrata*. *Erythranthe* of Asia and the Americas has also been previously consistently placed in *Mimulus*, apart from Greene's (1885) inclusion of some species in *Eunanus*. This group (our *Erythranthe*) is Grant's (1924) subgenus *Synplacus* of *Mimulus*.

Table 1. Genera of Phrymaceae adopted, with numbers of named and unnamed species and new species combinations, together with the historic application of generic and infrageneric names to them in selected significant global and regional taxonomic works. Bracketed are their infrafamilial placements in Scrophulariaceae ("S."), including Brown's "sections." Works in grey are regional or not covering all representatives known at time.

Our genera 2012 Phrymaceae (world)	New combi-nations	Total species (named, un-named)	Brown 1810 Scrophularinae (Australia)	Bentham 1835 Scrophularineae (India; also world *Mimulus*)	Bentham 1846 Scrophulariaceae; Schauer 1847 Phrymaceae (world)	Bentham & Hooker 1876 (May) Scrophularineae, Verbenaceae (world)	A. Gray 1876a (Dec) ➔ 1876b (Dec) *Mimulus* (N. Amer.)	Greene 1885 ➔ *Mimulus* and allies (N. Amer.)	A. Gray 1886a ➔ 1886b) Scrophulariaceae (N. Amer.)	Wettstein 1891 ➔ 1897 Scrophulariaceae; Briquet 1895 Phrymaceae (world)	A.L. Grant 1924 *Mimulus* (Scroph.) (world)	Barker 1982, etc. ➔ Barker & Harden 1999 Scrophulariaceae (Australasia)	Fischer 2004 Scrophulariaceae ("alternative family") (world; no spp. listed)
***Mimulus* s. str.**	-	7 (7, -)	*Mimulus* (S. - Sect. II. Stamina 4 antherifera)	*Mimulus* (S. - Gratioleae)	*Mimulus* § ***Erecti***, § ***Prostrati*** (S. - Antirrhinideae – Gratioleae – Eugratioleae)	*Mimulus* sect. *Eumimulus* (S. - Gratioleae - Mimuleae)	*Mimulus* § *Eumimulus*	*Mimulus* § *Eumimulus*	*Mimulus* § *Eumimulus* (S. - Antirrhinideae - Gratioleae)	*Mimulus* sect. *Eumimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Mimulus (subg. Synplacus) sect. Eumimulus, sect. Paradanthus*	*Mimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Mimulus* (S. - "Phrymaceae" – Mimuleae)
Thyridia gen. nov.	1	1 (1, -)	*Mimulus* (S. - Sect. II. Stamina 4 antherifera)	*Mimulus* (S. - Gratioleae)	*Mimulus* § ***Prostrati*** (S. - Antirrhinideae – Gratioleae – Eugratioleae)	*Mimulus* sect. *Eumimulus* (S. - Gratioleae - Mimuleae) by citation "Benth. in DC."	-	-	-	*Mimulus* sect. *Eumimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Mimulus (subg. Synplacus) sect. Paradanthus*	*Mimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	? *Mimulus* (S. - "Phrymaceae" – Mimuleae)
Microcarpaea	-	2 (2, -)	***Microcarpaea*** (S. - Sect. I. Stamina duo antherifera. Capsula bilocularis)	*Microcarpaea* (S. - Gratioleae)	*Microcarpaea* (S. - Rhinanthideae – Buddlieae)	*Microcarpaea* (S. - Gratioleae - Limoselleae)	-	-	-	*Microcarpaea* (S. - Anthirrhinoideae-Gratioleae-Limosellinae)	-	*Peplidium / Microcarpaea* ➔ *Microcarpaea* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Microcarpaea* (S. - "Phrymaceae" - Microcarpeae)
Uvedalia	1	4 (2, 2)	***Uvedalia*** (S. - Sect. II. Stamina 4 antherifera)	*Uvedalia* (S. - Gratioleae)	*Mimulus* § ***Erecti*** (S. - Antirrhinideae – Gratioleae – Eugratioleae)	*Mimulus* sect. *Eumimulus* (S. - Gratioleae - Mimuleae) by citation "Benth. in DC."	-	-	-	*Mimulus* sect. *Eumimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Mimulus (subg. Synplacus) sect. Eumimulus*	*Mimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	? *Mimulus* (S. - "Phrymaceae" – Mimuleae)
Peplidium	-	14 (4, 10)	-	*Peplidium* (S. - Gratioleae)	*Peplidium* (S. - Antirrhinideae – Gratioleae – Lindernieae)	*Peplidium* (S. - Gratioleae - Limoselleae)	-	-	-	*Peplidium* (S. - Anthirrhinoideae-Gratioleae-Limosellinae)	-	*Peplidium / Microcarpaea* ➔ *Peplidium* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Peplidium* (S. - "Phrymaceae" - Microcarpeae)
***Elacholoma* (*E. hornii*)**	1	3 (2, 1)	-	-	-		-	-	-	-	-	*Elacholoma* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Elacholoma* (S. - "Phrymaceae" - Microcarpeae)
***Elacholoma* (*E. prostrata*)**	-	see above	-	-	*Mimulus* § ***Erecti***, § ***Prostrati*** (S. - Antirrhinideae – Gratioleae – Eugratioleae)	*Mimulus* sect. *Eumimulus* (S. - Gratioleae - Mimuleae) by citation "Benth. in DC."	-	-	-	*Mimulus sect. Eumimulus (S. - Anthirrhinoideae-Gratioleae-Mimulinae), partly*	*Mimulus (subg. Synplacus) sect. Paradanthus*	*Mimulus* (S. - Anthirrhinoideae-Gratioleae-Mimulinae)	*Mimulus* (S. - "Phrymaceae" – Mimuleae)

Table 1, continued.

Our genera 2012 Phrymaceae (world)	New combi-nations	Total species (named, un-named)	Brown 1810 Scrophularinae (Australia)	Bentham 1835 Scrophularineae (India; also world *Mimulus*)	Bentham 1846 Scrophulariaceae; Schauer 1847 Phrymaceae (world)	Bentham & Hooker 1876 (May) Scrophularineae, Verbenaceae (world)	A. Gray 1876a (Dec) ➔ 1876b (Dec) *Mimulus* (N. Amer.)	Greene 1885 ➔ *Mimulus* and allies (N. Amer.)	A. Gray 1886a ➔ 1886b) Scrophulariaceae (N. Amer.)	Wettstein 1891 ➔ 1897 Scrophulariaceae; Briquet 1895 Phrymaceae (world)	A.L. Grant 1924 *Mimulus* (Scroph.) (world)	Barker 1982, etc. ➔ Barker & Harden 1999 Scrophulariaceae (Australasia)	Fischer 2004 Scrophulariaceae ("alternative family") (world; no spp. listed)
Glossostigma	-	8 (5, 3)	-	-	*Glossostigma*, ***Tricholoma*** Benth. [non (Fr.) Staude] (S. - Rhinanthideae – Sibthorpieae)	*Glossostigma* (S. - Gratioleae - Limoselleae)	-	-	-	*Glossostigma* (S. - Anthirrhinoideae- Gratioleae- Limosellinae)	-	*Glossostigma* (S. - Anthirrhinoideae- Gratioleae- Mimulinae)	*Glossostigma* (S. - "Phrymaceae" - Microcarpeae)
Phryma	-	1 (1, -)	-	-	*Phryma* (Phrymaceae)	*Phryma* (Verbenaceae – Phrymeae)	-	-	*Phryma* (Verbenaceae)	*Phryma* (Phrymaceae)		-	"Phrymaceae" (in note: no tribal placement)
Hemichaena	-	5 (5, -)	-	-	*Diplacus*, *Leucocarpus* (S. - Antirrhinideae – Cheloneae)	*Hemichaena* (S. - Cheloneae)	-		-	*Berendtia* ➔ *Berendtiella*, *Hemichaena*, *Mimulus* sect. *Diplacus* (S. - Antirrhinoideae- Cheloneae)	*Berendtia; Mimulus* (subg. *Schizoplacus*) *sect. Tropanthus*	-	*Hemichaena (syn. Berendtia, Berendtiella)* (S. - "Phrymaceae" – Leucocarpeae)
***Mimetanthe* (*M. pilosa*)**	-	1 (1, -)	-	-	*Herpestis* § ***Mimuloides*** (S. - Antirrhinideae – Gratioleae – Eugratioleae))	*Mimulus* sect. *Mimuloides* (S. - Gratioleae - Mimuleae)	*Mimulus* § *Mimuloides*	*Mimulus* § *Mimuloides* ➔ ***Mimetanthe***	*Mimulus* § *Mimuloides* (S. - Antirrhinideae - Gratioleae)	*"Mimelanthe"* (S. - Anthirrhinoideae- Gratioleae- Herpestidinae)	*Mimetanthe*	--	*Mimetanthe* (S. - "Phrymaceae" – Mimuleae)
Diplacus	34	46 (46, -)	-	*Mimulus* (S. - Gratioleae)	*Diplacus*, *Eunanus*, *Mimulus* § ***Speciosi*** (S. – Antirrhinideae – Gratioleae – Eugratioleae)	*Mimulus* sect. *Eunanus, sect. Diplacus* (S. - Gratioleae - Mimuleae)	*Mimulus* § *Eunanus*, § *Diplacus* ➔ also **§*Oenoe***	*Diplacus; Eunanus (sect. Oenoe, Eunanus, Mimulastrum)*	*Mimulus* § *Diplacus*, § *Eunanus* ➔ also § *Oenoe*, § *Mimulastrum* (S. – Antirrhini-deae - Gratioleae)	*Mimulus* sect. *Diplacus*, sect. *Oenoe*, sect. *Eunanus*, sect. *Mimulastrum* (S. - Anthirrhinoideae- Gratioleae- Mimulinae)	*Mimulus* (subg. *Schizoplacus*) sect. *Eunanus, sect. Oenoe, sect. Diplacus*, sect. *Mimulastrum*, sect. *Pseudoenoe*	-	*Mimulus* (S. - "Phrymaceae" - Mimuleae)
Leucocarpus	-	1 (1, -)	-	-	*Leucocarpus* (S. - Antirrhinideae – Cheloneae	*Leucocarpus* (S. - Cheloneae)	-	-	-	*Leucocarpus* (S. - Antirrhinoideae- Cheloneae)	*Leucocarpus*	-	*Leucocarpus* (S. - "Phrymaceae" – Leucocarpeae)
Erythranthe	104	111 (111, -)	-	*Mimulus* (S. - Gratioleae) check	*Mimulus* § ***Speciosi***, § ***Teneri*** (S. - *Antirrhinideae – Gratioleae* – Eugratioleae)	*Mimulus* sect. *Eumimulus* (S. - Gratioleae - Mimuleae)	*Mimulus* § *Eumimulus*	*Eunanus* sect. *Eunanus; Mimulus* (*§ Erythranthe, § Simiolus*)	*Mimulus* § *Eumimulus* (S. - Antirrhinideae - Gratioleae)	*Mimulus* sect. *Eumimulus* (S. - Anthirrhinoideae- Gratioleae- Mimulinae)	*Mimulus (subg. Synplacus) sect. Erythranthe, sect. Simiolus, sect. Paradanthus*	-	*Mimulus* (S. - "Phrymaceae" – Mimuleae)
Total	**139**	**188 (188, 4)**											

Our classification diverges most radically in the two largest genera, *Diplacus* and *Erythranthe*. *Diplacus* has been subject to varied interpretations, ranging from an infrageneric group within *Mimulus* to 2–4 groups sometimes recognized within a broader *Mimulus*, at other times in major part recognized as three genera — a narrower *Mimulus*, *Diplacus*, and *Eunanus* Benth. *Diplacus* corresponds largely to Grant's (1924) subgenus *Schizoplacus* of *Mimulus*. *Erythranthe* has generally been narrowly circumscribed as the group of mostly red-flowered species including *Mimulus cardinalis* and its close relatives.

Hemichaena historically has been poorly known and sometimes included in *Mimulus*. The genus *Berendtiella* was merged with it by Thieret (1972b). Apart from *Berendtiella*, only two other genera described in the past 150 years are not recognized here: *Eunanus* Benth. (1846) in its original concept only, which is our section of that name in *Diplacus*, and *Tricholoma* Benth., here merged into *Glossostigma*.

At a family level *Phryma* and *Elacholoma* have been doubtfully placed since their discovery. The relationship of *Phryma* with *Mimulus* in the Scrophulariaceae was established by recent molecular study (Beardsley & Olmstead 2002), that of *Elacholoma* with the work of Barker (1982).

In terms of tribal placements of genera in Scrophulariaceae, *Mimulus* and its sometimes recognized generic relatives *Uvedalia*, *Mimetanthe*, *Diplacus*, and *Eunanus* have been consistently placed in the tribe Mimuleae (or Gratioleae subtribe Mimulinae). The genera *Microcarpaea*, *Peplidium*, and *Glossostigma* were traditionally separated tribally in the Scrophulariaceae in the Limoselleae (or Gratioleae subtrib. Limosellinae), a repository for often small semi-aquatics of obscure relationships, until the work of Barker (1982). *Leucocarpus* and *Hemichaena* were generally placed in the tribe Cheloneae until the work of Grant (1924).

Rank and typification of genera and sections

Several species groups at sectional rank in *Mimulus* have been recognized in previous studies (e.g., Grant 1924; Pennell 1947; Vickery 1966a, 1966b, 1969, 1974, 1997; Beardsley 2003; Beardsley et al. 2004; Thompson 2005; Whittall et al. 2006) and are clearly typified. Some sections have been named but never typified and are provided here with lectotypes. Some of the species groups are provided here for the first time with formal names at sectional rank.

The § symbol was used for infrageneric groups in all the key historic works dealt with here, with varying clarity as to whether they had a consistent and specified rank. Infrageneric ranks were not or rarely clearly specified in the works of the 19th Century. These names of uncertain rank are validly published under Rule 35.3 of the ICN and are available as basionyms for their use with specified rank.

Within *Mimulus*, Bentham (1846) named four species groups using plural adjectives preceded by the § symbol. In the genera *Linaria* (loc.cit., pp. 266–288) and *Herpestis* (loc.cit., pp. 392–401), Bentham explicitly designated sections using substantives and, using the same convention (the § symbol and plural adjective), delineated subsidiary species groups that could justifiably be regarded either as subsections or series. In the absence of clarity as to which rank Bentham intended, the names are lectotypified but maintained without rank.

Bentham and Hooker (1876) clearly specify that their groups were sections, but Gray (1876a, 1876b, 1884, 1886a, 1886b) and Greene (1885) rarely applied a rank term. When they used a term it was generally section and only in discusson. Gray uses the term section in notes in his second publication, and it was used by Lemmon in publishing Gray's sect. *Mimulastrum* (Gray 1884), but Gray (1886b) also used subgenera in discussion (describing *Mimulus* as "Polymorphous, but better

retained entire under five subgenera"). Greene indicated that his infrageneric groups were sections in discussion under only one of his genera, *Eunanus*. Grant (1924) clearly and consistently applied the ranks (subgenus and section) to each of her infrageneric taxa, a convention followed for example by Pennell (1935, 1947, 1951) and made mandatory from 1953 (ICN Art. 35).

Species delimitation

The authors of this paper have adopted convergent approaches to species delimitation in studies of various parts of the family, basing their decisions on herbarium and field studies and specimen sampling of variation within and between populations and observations of sympatric and parapatric interactions among taxa.

The species of *Diplacus* have received recent detailed taxonomic study (McMinn 1951; Beeks 1962; Ezell 1970; Waayers 1996; Tulig 2000; Tulig & Clark 2000; Thompson 2005; Tulig & Nesom 2012). Within *Diplacus* sensu lato, the mostly shrubby or semi-shrubby entities (sect. *Diplacus* or sometimes segregated as the separate genus *Diplacus* sensu stricto) clearly arose from ancestors of annual duration. These entities have been treated taxonomically in widely varying ways; the concepts here are those of Tulig (2000; formally summarized by Tulig and Nesom (2012). Also within *Diplacus*, *Eunanus* has previously been segregrated as a genus but is treated here at sectional rank.

Species concepts in *Erythranthe* have remained more controversial or poorly understood, despite a treatment by Thompson (1993). The present overview is accompanied by detailed studies of the *Mimulus moschatus* alliance (sect. *Mimulosma*, sensu Nesom 2012b), the *Mimulus guttatus* group (sect. *Simiolus*, Nesom 2012a), and the *Mimulus inconspicuus* group (sect. *Achylopitheca*, Nesom 2012c). A detailed study of the *Mimulus palmeri* lineage (*Erythranthe* sect. *Paradantha* sensu stricto) is being conducted by Fraga (2011 and in prep.).

For precise reference to species and species groups in taxonomic treatments for the Flora of North America North of Mexico (FNANM; Nesom with Fraga and Tulig, in prep.) as well as in further detailed studies in various species groups, the species of *Diplacus* and *Erythranthe* in the classification presented here are divided into groups that primarily reflect the phylogenetic hypothesis of Beardsley et al. (2004, Figs. 1/5 and 2/4). Species not included in the molecular analysis are interpolated in the classification on the basis of morphological features.

Pennell (1951) treated 107 species of *Mimulus* from the Pacific States, but other treatments, particularly including those by Thompson (1993, 2005), have placed a number of earlier-accepted taxa in synonymy, thus considerably reducing the number of species. Many recent studies of evolutionary processes in *Mimulus*, however, emphasize that reproductive isolating mechanisms may sometimes evolve relatively quickly among populations (e.g., Wu et al. 2007), and our own studies have confirmed that recognition of conservative numbers of species in some groups do not accurately represent the variation patterns of *Mimulus* sensu lato. In the *Mimulus palmeri* lineage (here as *Erythranthe* sect. *Paradantha*) (Fraga 2011 and in prep.), studies in field and lab have shown that at least five species remain to be described. In the *Mimulus guttatus* group (here as *Erythranthe* sect. *Simiola*), the *M. floribundus* group (here as *Erythranthe* sect. *Mimulosma*), and the *M. inconspicuus* group (here as *Erythranthe* sect. *Achlyopitheca*), narrower species concepts of earlier studies by E.L. Greene, A.L. Grant, and F.W. Pennell have been corroborated in some cases (Nesom 2012b, 2012a, 2012c).

A revision of the the Australasian-centered genera and *Mimulus* sensu stricto (Barker in prep.) will adopt the generic concepts in this paper and will result in formal description of species denoted by informal phrase-names in Beardsley and Barker (2005), further unnamed species, confirmation of

generic placement, and erection of infrageneric taxa, particularly in *Peplidium*. To date genera and species have been described in a series of regional and state floras and associated publications (Barker 1981, 1982, 1983, 1986, 1990, 1992a, 1992b; Barker & Harden 1992, 1999). Bean (1997, 2003) has also described single species in *Microcarpaea* and *Mimulus* sensu stricto. The species numbers for the Australasian-centered genera are those given in the account of Beardsley and Barker (2005).

Further work under way is investigating the basis of significant homoplasy in striking synapomporphies of the seed surface and reduction of stigma lobes and anther cells (cf. Beardsley & Barker 2005).

Ovary and fruit variation

The morphological distinction of *Hemichaena*, *Mimetanthe*, and *Diplacus* within Phrymaceae is remarkable — parietal placentation in this lineage (clade C) apparently is a specialization arising directly from axile placentation characteristic of the rest of the family (Fig. 2). These differences were described by Grant (1924) and Thompson (2005) and confirmed here. Presumably the development of parietal placentation has happened by (a) adnation of placentae to lateral walls, (b) loss of the septum, and (c) a shift in position of dehiscence. In distinguishing between *Erythranthe* and *Diplacus*, the difference in placentation provides an easily observed and unequivocal distinction.

In addition to the radical gynoecial modification in the *Diplacus* lineage, another has occurred in *Phryma*, which has a unilocular ovary (pseudo-monomerous, 2-carpellate with 1 carpel reduced developmentally) with a single ovule with basal placentation.

Two of the three main variants are shown in Figure 2.

A. Placentation axile, placentae fused in the basal half or for the whole length, remaining fused in fruit dehiscence; capsule dehiscent to base along outer suture or both sutures.

B1. Placentation parietal, placentae separate (sometimes appressed but not fused), remaining attached to the walls and spread apart in fruit dehiscence; capsule dehiscent along the distal half of the inner (upper) suture to only distally along the outer (lower) suture.
B2. Placentation parietal, placentae fused and also remaining attached to the walls, not spread apart in fruit dehiscence; capsule dehiscent along distal third of both sutures.

C. Placentation basal; fruit indehiscent (achene).

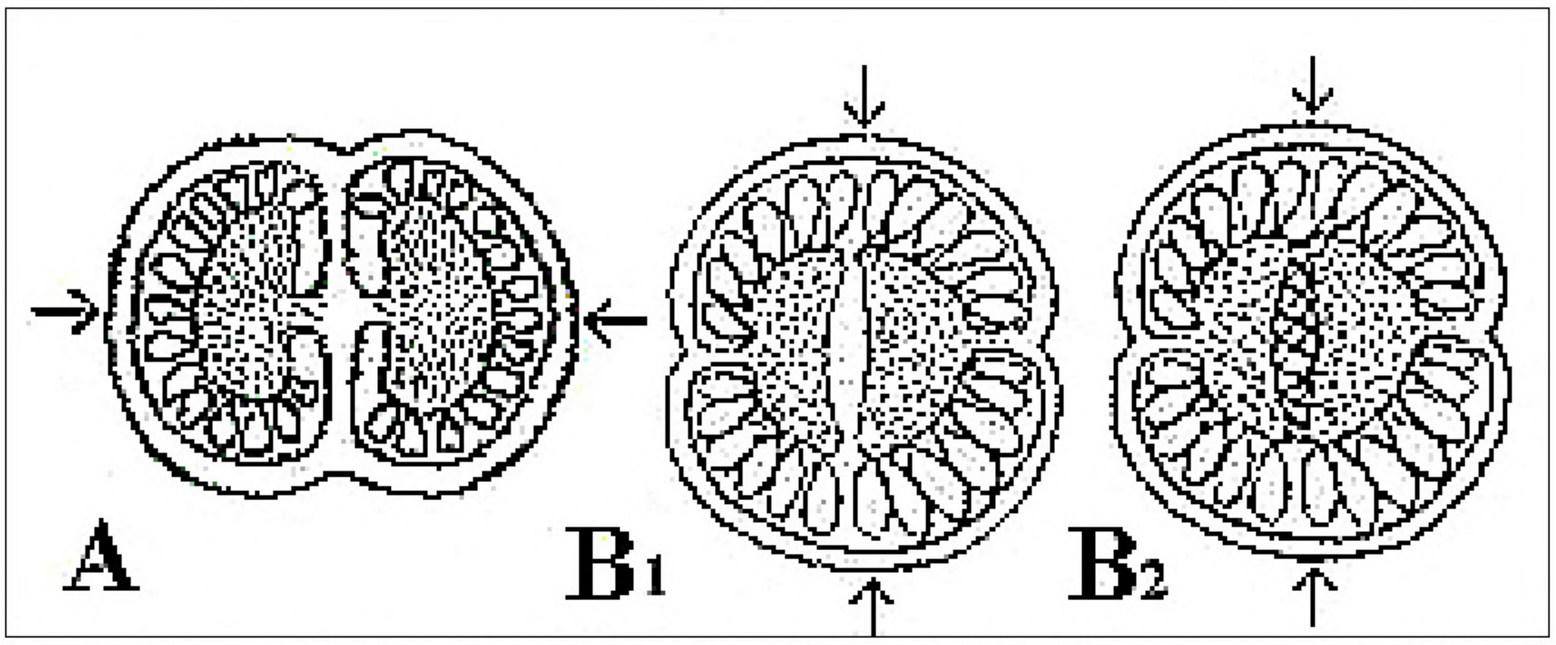

Figure 2. Representative ovary cross-sections (diagrammatic) Phrymaceae, not including *Phryma*. Arrows mark locations of dehiscence in capsules. A. Placentation axile: *Mimulus*, *Thyridia*, *Microcarpaea*, *Uvedalia*, *Peplidium*, *Elacholoma*, *Glossostigma*, *Leucocarpus*, and *Erythranthe*. B1. Placentation parietal: *Hemichaena* and *Diplacus*. B2. Placentation parietal (placentae fused at least proximally): *Mimetanthe*. In *Phryma*, the ovary is unilocular and placentation of the single ovule is basal.

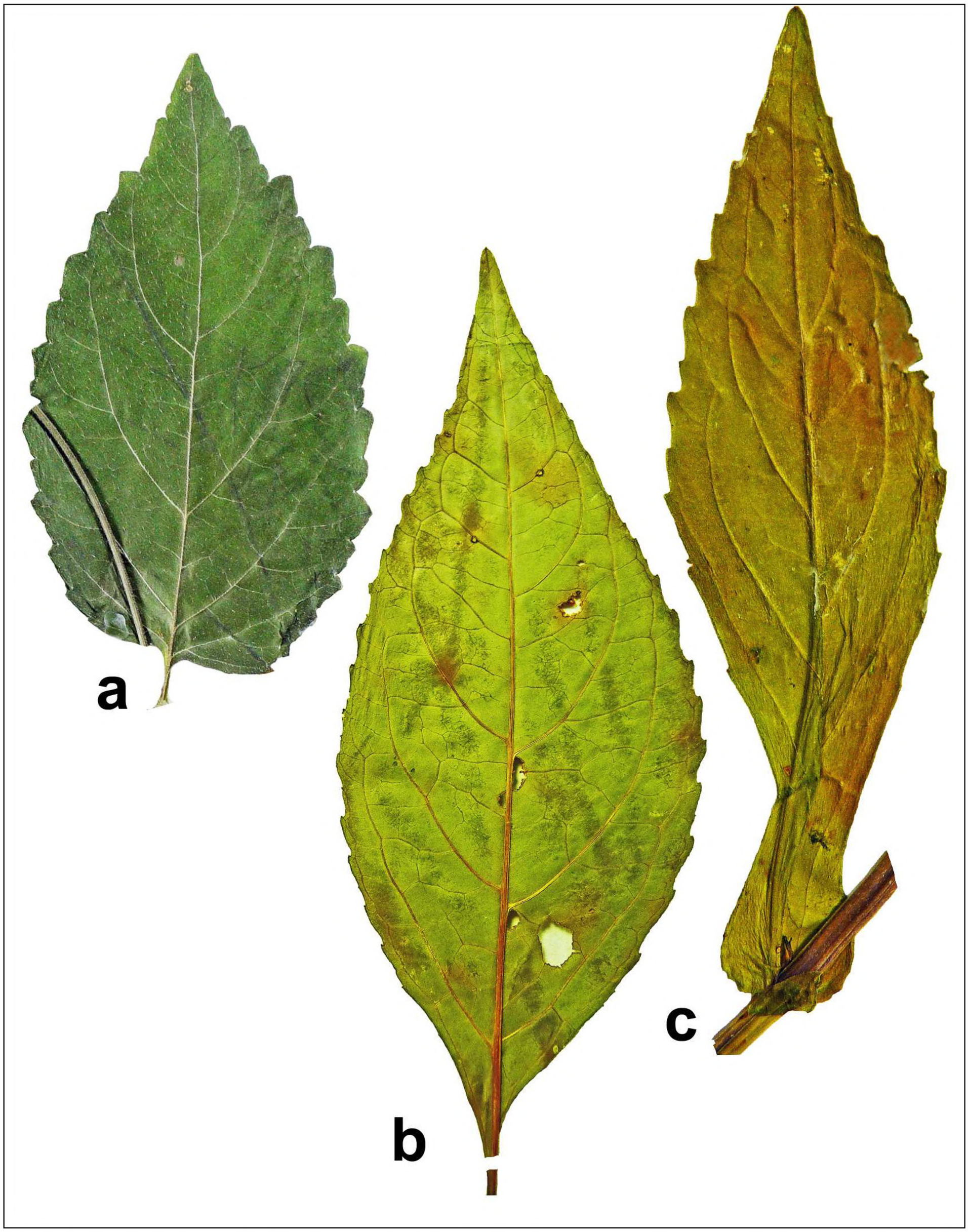

Figure 3. Leaf venation in Phrymaceae. A. **Mixed craspedodromous**: (a) *Phryma leptostachya.* B. **Weak brochidodromous**: (b) *Mimulus alatus*, (c) *Mimulus ringens.* Examples are not at the same size scale.

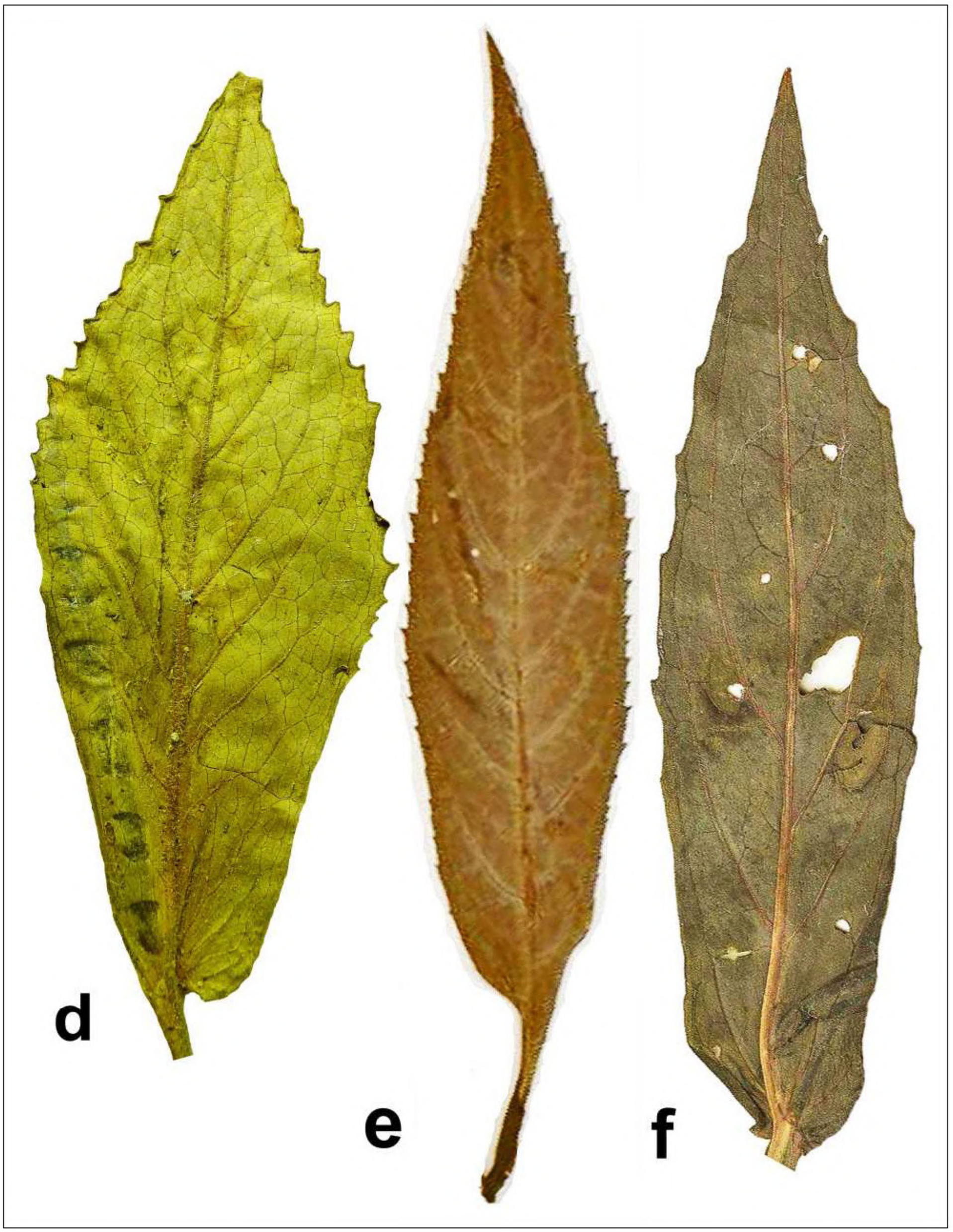

Figure 4. Leaf venation in Phrymaceae. **Eucamptodromous**: (d) *Hemichaena fruticosa*, (e) *Leucocarpus perfoliatus*, (f) *Erythranthe bracteosa*. Examples are not at the same size scale.

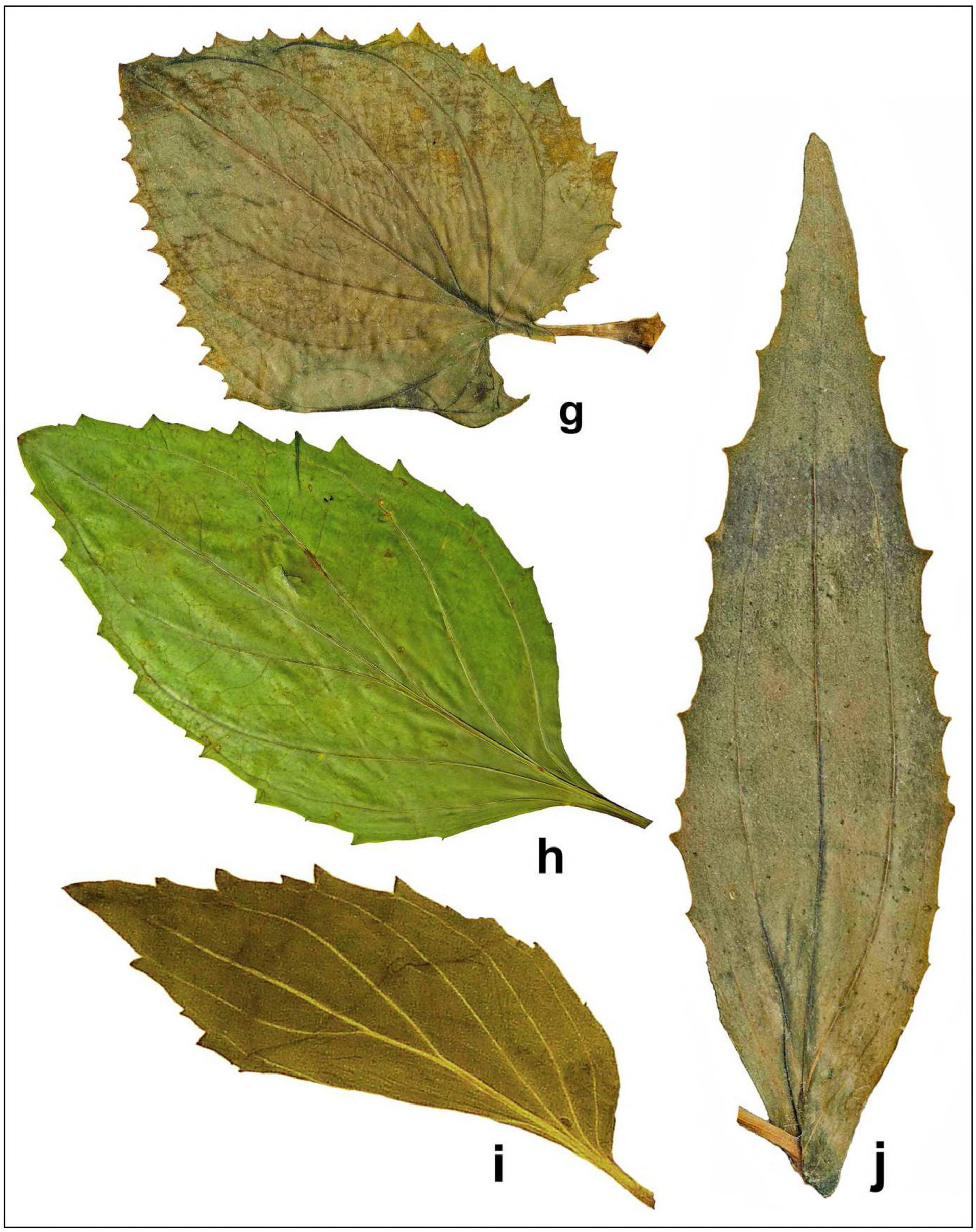

Figure 5. Leaf venation in Phrymaceae. **Basal to near-basal acrodromous**: (g) *Erythranthe decora*, (j) *Erythranthe nelsonii* (3-nerved). **Suprabasal acrodromous to eucamptodromous**: (h) *Erythranthe dentata*, (i) *Erythranthe sinoalba*. Examples are not at the same size scale.

Leaf venation

Leaf venation in *Phryma* (Fig. 3a) seems best described as **mixed craspedodromous** (see Hickey 1973 for terms and definitions). It does not appear to be closely matched by any other Phrymaceae — rather it is more similar to the pattern often seen in mints and verbenas, where *Phryma* has traditionally been placed.

Venation is **acrodromous** in *Erythranthe*, *Diplacus*, and *Mimetanthe* and **eucamptodromous** (with more numerous suprabasal secondary veins, thus appearing pinnate) in *Leucocarpus* and *Hemichaena*, both patterns with the secondary veins arching convergently toward the apex and essentially remaining distinct their whole length. **Acrodromous** variants in *Erythranthe* and *Diplacus* have veins all basal (thus appearing palmate, Fig. 4e) or reduced to 1-nerved (**hyphodromous**) or 3-nerved in species with smaller leaves and even in larger leaves, as in Fig. 4f. When some veins tend to be suprabasal, venation appears to vary between palmate and subpinnate to pinnate (Figs. 5g, h, i). Even in the largest and longest leaves, secondary veins usually remain distinct, although an occasional connecting vein may develop.

The two North American species of *Mimulus* can be separated from *Erythranthe* and from Southern Hemisphere *Mimulus* sensu stricto by their **weak brochidodromous** leaf venation (Fig. 3b, c), with secondary veins weakly joining at the apices. It seems likely that this pattern is homologous with the essentially acrodromous/eucamptodromous pattern found in the rest of the family (except *Phryma*).

Ecological terminology

The family occupies substrates that are permanently, seasonally, or briefly inundated in fresh water. *Aquatic* indicates that the plant begins and largely completes its life cycle in water. *Semi-aquatic* is used here to mean that a plant occupies seasonally or ephemerally aquatic habitats but persists on dried-out substrates where it completes its life cycle. *Terrestrial* means that the plant is not dependent on an initial submerged phase of the life cycle but may occur on moist exposed substrate.

Treatments of the genera and sections

Descriptions of genera are consistent within the main lineages but may differ slightly between them where measurements are lacking for features not traditionally used diagnostically. However, we have tried to be consistent in important diagnostic characters.

Lists of species included for each section are separated by geography using traditional widely used geographical regions, but the boundaries of the Flora of North America North of Mexico are specially adopted.

Genera and infrageneric groups of former classifications often have a very different circumscription from the genera and sections of our classification (see above). As well as citing the protologue reference, in many instances we also cite literature in which other taxonomic circumscriptions were adopted (see Appendix).

PHRYMACEAE Schauer in DC. Prod. 11: 520. 1847, nom. cons

Annual or perennial herbs, secondarily woody; iridoids absent, possibly sometimes present. **Leaves** opposite with margins entire or toothed, gland-dotted (punctate) or not. **Flowers** with hypogyous parts, in racemes, rarely solitary or in axillary clusters of 2–3; bracteoles absent. **Calyx** tubular, toothed, the tube ribbed or winged below teeth, rarely smooth. **Corolla** zygomorphic, rarely secondarily sub-actinomorphic, the limb with two upper lobes and 3 lower lobes or 5 equal lobes, rarely reduced to 3–4 lobes, sometimes with palate of variable form and color. **Stamens** 4, didynamous, rarely reduced to 2, with straight filaments arising from corolla tube, the anthers subreniform, with 2 confluent cells, rarely reduced by fusion to 1, with pollen trinucleate; <10-colpate; each colpus with 2 orae, or irregularly synaperturate (± spiraperturate, sect. *Simiola*, see Argue 1980). **Gynoecium**: nectary sometimes present; carpels 2, many-ovulate developing equally, rarely 1, single ovulate, the other vestigial, placentiation axile, less often parietal, rarely sub-basal, the style terminal, the stigma 2-lobed, with lobes laminate, often sensitive, rarely (*Elacholoma hornii*) linear and probably not sensitive), sometimes the adaxial lobe shorter, sometimes reduced to a vestige. **Fruit** a loculicidal capsule, dehiscent, rarely fracturing, rarely a berry, borne in a persistent calyx. **Seeds** small, many, rarely 1 (in *Phryma*), surface reticulate and sometimes ribbed or winged, smooth, or tessellate; endosperm present or almost absent, cotyledons convolute. n = 7-10, 14, 22, etc. Native to the Americas, Asia, Africa, and Australasia.

Pollen, wood, chemical, seed anatomy, cotyledon, and chromosome details are taken from the family description in APG II (Stevens 2001 onwards).

In the main section, the statements of synonymy give only homotypic synonyms. In the Appendix, summaries of taxonomic usage of generic and infrageneric names in previous literature are provided.

KEY TO THE GENERA OF PHRYMACEAE

1. Fruit a unilocular, 1-seeded achene; ovary 2-carpellate with 1 carpel reduced developmentally (pseudomonomerous) ..... 8. **Phryma**
1. Fruit a bilocular, many-seeded capsule or (*Leucocarpus*) a berry; ovary 2-carpellate.

2. Stigma 1-lamellate with a vestige of a second flap on the adaxial side of the style; anthers 1-celled.

3. Calyx not ribbed, 3-4-lobed, lobes unequal ..... 7. **Glossostigma**
3. Calyx 5-angled, 5-lobed, lobes equal.

4. Leaves linear, sessile, blades herbaceous, not fleshy; calyx not fleshy, lobes recurved, sharply acute, ciliolate; capsules loculicidal; seeds reticulate ..... 3. **Microcarpaea**
4. Leaves ovate to obovate to broadly obovate or spathulate, short-petiolate, the blade fleshy; calyx fleshy, lobes erect, bluntly acute to obtuse, glabrous or ciliolate; capsules loculicidal or tardily dehiscent by fracturing irregularly; seeds reticulate or ribbed with the ribs longitudinally rugose and with a row of areolae on each side ..... 5. **Peplidium**

2. Stigma 2-lamellate or 2-fid (sometimes one flap reduced); anthers 2-celled.

5. Placentation parietal; fruits apically attenuate.

6. Flowers in bracteolate, axillary cymes, short-pedicellate; leaf venation eucamptodromous ..... 9. **Hemichaena**
6. Flowers axillary and solitary, sessile to short-pedicellate or long-pedicellate; leaf venation acrodromous.

7. Fruit walls densely pustulate-glandular; placentae fused at least in proximal half; pedicels longer than the calyx; calyces with midveins low-rounded (not angled or winged) ..... 10. **Mimetanthe**
7. Fruit walls glabrous or at least eglandular; placentae distinct, not fused; pedicels shorter than the calyx or essentially absent; calyces with midveins angled or wing-angled ..... 11. **Diplacus**

5. Placentation axile; fruits apically rounded to truncate.
8. Fruit a berry ..... 12. **Leucocarpus**
8. Fruit a loculidical capsule.

9. Corollas subactinomorphic, pedicels shorter than the calyx; plants prostrate; stigma 2-flapped or 2-terete ..... 6. **Elacholoma**
9. Corollas bilabiate (sometimes secondarily subactinomorphic), pedicels mostly usually distinctly longer than the calyx; plants prostrate to erect; stigma usually 2-flapped.

10. Leaves glandular-punctate; seeds ribbed, the ribs thick, longitudinally rugose, with a row of areolae along each side; plants semi-aquatic, prostrate or rarely erect herbs; capsules thick-walled, tardily dehiscent ..... 2. **Thyridia**
10. Leaves not glandular-punctate; seeds reticulate or tessellate, lacking ribs; plants terrestrial to semi-aquatic, mostly erect herbs; capsules thin-walled, readily dehiscent.

11. Leaves 1-nerved ..... 4. **Uvedalia**
11. Leaves palmately veined to pinnately veined.

12. Leaf venation weak brochidodromous (N. America) or basal acrodromous (S. Hemisphere); base chromosome number, x = 8, 11, 12 ..... 1. **Mimulus**
12. Leaf venation basal acrodromous to suprabasal-acrodromous; base chromosome number, x = 14, 15, 16 ..... 13. **Erythranthe**

I. MIMULUS L., Sp. Pl. Sp. 2: 634. 1753. **TYPE**: *Mimulus ringens* L. The genus as originally described by Linnaeus included only a single species.

Monavia Adans., Fam. Plant. 2: 211. 1763, nom. illeg. Superfluous when published, intended by Adanson as a replacement name for *Mimulus* L., which was listed as a synonym. Not *Mimulus* of Plinius, which was treated by Adanson as the name for *Rhinanthus* of Linnaeus. **TYPE**: *Mimulus ringens* L.

Cynorrhynchium J. Mitchell, Diss. Brevis. Princ. Bot. Zool. 29. 1769, nom. illeg. (includes type of an existing genus: ICN Art. 52.1). **NEOTYPE** (designated here): *Mimulus ringens* L. Although Pennell (1935, p. 112) wrote that the 1769 protologue "exactly repeated Mitchell's previous description in Acta Phys.-Med. Acad. Caes. Leop.-Francisc. Nat. Cur. 8: 207. 1748; only the genus was described, but by Linnaeus' reference in the Genera Plantarum [1754 (ed. 5), p. 283] to *Cynorrhynchium* as a synonym of *Mimulus*, Mitchell's plant was correctly identified with *M. ringens* L.," he did not effectively designate a neotype. The description by Linnaeus also incorporated much of the original by Mitchell.

Most of Mitchell's herbarium and types are in BM-Banks, with others in G, LINN, and OXF but a collection of *Mimulus* by Mitchell apparently is not among them.

Mimulus § *Erecti* Benth. in DC., Prodr. 10: 369. 1846, without indication of rank. **LECTOTYPE** (designated here): *Mimulus ringens* L. Bentham included, in part, *M. ringens*, *M. alatus*, *M. madagascariensis*, *M. gracilis*, *M. pusillus*, and *M. uvedaliae* in his taxon. There is no clear choice for lectotype; the species selected.here is one that Bentham had studied from adequate material.

Mimulus § *Prostrati* Benth. in DC., Prodr. 10: 373. 1846, without clear indication of rank. **LECTOTYPE** (designated here): *Mimulus orbicularis* Wall. ex Benth. Bentham included *M. orbicularis*, *M. repens*, and *M. prostratus*. He noted that these comprised "Species Asiaticæ

vel Australasicæ." This taxon has not been adopted subsequently or assigned a definite rank, and in global works these species have been consistently treated together. There is no clear choice for lectotype; the species selected here is one that Bentham had studied from adequate material.

Mimulus subg. *Synplacus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"). **LECTOTYPE** (designated here): *Mimulus ringens L.* Grant did not specify a type from among the four sections she included in subg. *Synplacus*. Typification of subg. *Synplacus* has not subsequently been made explicit and the subgenus has not been used to the exclusion of any sections or species among those with axile placentation. What species Grant may have had in mind as the type of subg. *Synplacus* is not clear — the choice here simply places the taxon as a synonym of *Mimulus* sensu stricto.

Perennial, rhizomatous, terrestrial or semi-aquatic. **Vestiture**: glabrous. **Stems** herbaceous, erect, 4-angled, winged in *M. alatus*. **Leaves** petiolate and thin-herbaceous (*M. alatus*) or fleshy (*M. orbicularis*), or sessile and semi-succulent, usually glandular-punctate, venation brochidodromous (*M. alatus*, *M. ringens*) or basal acrodromous (*M. aquatilis*, *M. strictus*) margins toothed. **Flowers** single, axillary at medial to distal nodes. **Fruiting pedicels** shorter or longer than calyces. **Fruiting calyces** erect, tube midveins angled to winged-angled. **Corollas** blue to violet, purplish, light pink, nearly white, or (*M. bracteosus*) yellow, deciduous, limbs strongly bilabiate and sagitally compressed. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** axile; **stigmas** bilamellate. **Fruits** many-seeded capsules with blunt or rounded to slighty emarginate apices, loosely enclosed in persistent calyx, included, bilocular, loculicidally dehiscent to base along outer suture or both sutures; placentae fused in the basal half or for the whole length, remaining fused in fruit dehiscence. **Seed** surface reticulate. **Chromosome numbers**, $2n$ = 16, 22, 24. **Species** 7.

(FNANM)

1. Mimulus alatus Sol. ex Ait., Hort. Kew. 2: 361. 1789.

2. Mimulus ringens L., Sp. Pl. 2: 634. 1753.

a. Mimulus ringens var. **ringens**

b. Mimulus ringens var. **colpophilus** Fernald, Rhodora 34: 119. 1932.

(AUSTRALIA)

3. Mimulus gracilis R. Br., Prodr. Fl. Nov. Holland. 439. 1810.

4. Mimulus aquatilis A.R. Bean, Austrobaileya 6: 550. 2003. (See comments below.)

(AFRICA, MADAGASCAR, INDIA)

5. Mimulus strictus Benth. , Scroph. Ind. 28. 1835. India, Africa

Mimulus angustifolius Hochst. ex A. Rich., Tent. Fl. Abyss. 2: 119. 1850.

6. Mimulus madagascariensis Benth. in DC., Prodr. 10: 369. 1846. Madagascar.

Limnophila torenioides Baker, J. Bot. 20: 221. 1882.

(ASIA)

7. Mimulus orbicularis Wall. ex Benth., Scroph. Ind., 29. 1835. Vietnam Cambodia, Laos, Thailand, Myanmar. See comments below, under *Peplidium*.

Material of *Mimulus gracilis* from Australia differs from the dozen African and Indian specimens seen in its finer stems, finer roots, smaller, narrower, entire or almost entire leaves with a cuneate base, and its calyces densely pubescent inside and shortly lobed (Barker pers. obs.). This coincides with Pennell's (1943) observations. Pennell considered that the African-Indian plant might differ by its white or pale blue corollas from the blue-purple corollas of the Australian species, but it is based on limited observation. Pennell's resurrection of *M. strictus* for African and Indian

occurrences of *M. gracilis* has generally gone unrecognized but was followed by Yamazaki (1985) for Indo-China.

Only *Mimulus ringens* and *M. gracilis* have been subject to molecular analysis and they form the basis for the phyletic position of this group. The morphological and molecular attributes of the other species retained in *Mimulus* sensu stricto are being reviewed as they show quite different leaf and/or floral attributes. *Mimulus madagascariensis* is very different in leaf morphology, while the floating aquatic *M. orbicularis* has ecological and morphological aspects of *Peplidium* (Barker pers. obs.). Bean (2003) hypothesized that *M. aquatilis* of northeastern Australia is closely related to *M. gracilis*, but while included here, its sessile, palmately veined leaves seem out of place in narrowly defined *Mimulus* (Nesom pers. obs.). A relationship of *M. aquatilis* with *Erythranthe* sect. *Sinopitheca* might be suspected, but the Australian geography and punctate leaves of *M. aquatilis* are out of place in *Erythranthe*.

Despite the different chromosome numbers of the two American species (*Mimulus ringens*, $2n = 16, 24$; *M. alatus*, $2n = 22$) and strikingly different morphology, these two have been reported to form natural hybrids (Windler et al. 1976).

II. **THYRIDIA** W.R. Barker & Beardsley, **gen. nov. TYPE:** *Thyridia repens* (R. Br.) W.R. Barker & Beardsley

Validating diagnosis. A new genus differing from *Mimulus* sensu stricto by its ribbed seeds with a row of window-like areolae on each side of the ribs and from species of *Peplidium* with similar seeds by its bilabiate corolla with closed palate, its 2-celled anthers, and its bilamellate stigma.

Annual or perennial, semi-aquatic **herbs**, not rhizomatous. **Vestiture**: glabrous. **Stems** usually prostrate, rooting at nodes and forming mats, when submerged erect to 20 cm high and/or with erect branches arising from prostrate parts. **Leaves** semi-succulent, ovate to elliptic-oblanceolate, 2–6 mm, hyphodromous (1-nerved), sessile to subsessile, often cordate, distinctly glandular-punctate, margins entire. **Flowers** single, axillary in sporadic nodes, subsessile to pedicellate. **Fruiting pedicels** short to long. **Calyces** 3–5 mm long, ribbed, lobes shortly deltate. **Corollas** blue-purple, with a white and yellow palate; tube-throats funnelform, 5–7(–10) mm, limbs bilabiate, mouth closed by palate. **Stamens** 4; anthers 2-celled. **Ovaries** 2-locular; **placentation** axile; **stigma** bilamellate. **Fruits** loculicidally dehiscent, thick-walled capsules. **Seed** surface thick-ribbed, the ribs with a row of areolae along each side. **Chromosome number**, $2n = 20$. **Species** 1. Australia, New Zealand.

1. Thyridia repens (R. Br.) W.R. Barker & Beardsley, **comb. nov.**. *Mimulus repens* R. Br., Prodr. Fl. Nov. Holland. 432. 1810.
Mimulus colensoi Kirk, Trans. & Proc. New Zealand Inst. 3: 179 1871.

The generic name is derived from the Greek *thyris* (diminutive *thyridios*, denoting small door or window; Brown 1956), alluding to the row of window-like areolae along either side of the longitudinal ribs of the seed surface.

Thyridia has the floral parts of *Mimulus* sensu stricto, with a 5 ribbed tubular calyx, bilabiate corolla with a closed palate, didynamous anthers with 2 confluent cells, and a bilobed stigma. Separating it, however, are its gland-dotted fleshy leaves and its distinctive seed that has broad ribs with fine longitudinal lines on the outer face; these ribs have a row of areolae each side. These seed features are surely highly derived compared with the reticulate seed of *Mimulus* sensu stricto and *Microcarpaea*, *Elacholoma*, *Glossostigma* and elsewhere in the family. Similar seeds are also found

in some species of *Peplidium*, including *P. foecundum* W.R. Barker and several unnamed species. Gland-dotted fleshy leaves are found in other unnamed *Peplidium* species.

III. **MICROCARPAEA** R. Br., Prodr. Fl. Nov. Holland., 435. 1810. **TYPE**: *Microcarpaea muscosa* R. Br., nom. illeg. (= *Microcarpaea minima* (K.D. Koenig ex Retz.) Merrill), the only species in the protologue.

Semi-aquatic, annual, not rhizomatous, glabrous **herbs**. **Vestiture**: glabrous to sparsely eglandular hairy. **Stems** prostrate to procumbent, to over 10 cm long. **Leaves** sessile, hyphodromous or suprabasal acrodromous (3-nerved), not glandular-punctate, margins entire. **Flowers** axillary at medial to distal nodes, sessile to subsessile, rarely long pedicellate. **Fruiting pedicels** short to long. **Calyces** 2–3 mm, 5-ribbed, with 5 lobes spreading-reflexing at maturity. **Corollas** tiny, tube-throats cylindric, 1.5–2.3 mm, barely or not at all exserted from calyx. **Stamens** 2; anthers 1-celled. **Ovaries** 2-locular; **placentation** axile; **stigma** unilamellate through reduction of adaxial lobe to a vestige. **Fruits** bilocular, loculicidally dehiscent, thin-walled capsules; septum splitting down midline, each part attached to the valve. **Seed** surface reticulate. **Chromosome number** unknown. **Species** 2.

Microcarpaea minima is widespread — occurring in China, Taiwan, India, Indonesia, Japan, Korea, Malaysia, Thailand, Vietnam, and Australia — while *Microcarpaea agonis* is endemic to Queensland, Australia.

1. **Microcarpaea minima** (K.D. Koenig ex Retz.) Merrill, Philipp. J. Sci. 7: 100. 1912. *Paederota minima* K.D.Koenig ex Retz, Obs. Bot. 5: 10. 1788
   Microcarpaea muscosa R. Br., Prodr. Fl. Nov. Holland. 435. 1810, nom. illeg.
2. **Microcarpaea agonis** A.R. Bean, Austrobaileya 5: 149. 1997.

IV. **UVEDALIA** R. Br., Prodr., 440. 1810. **TYPE**: *Uvedalia linearis* R. Br., the only species in the protologue.

Terrestrial, annual **herbs**, not rhizomatous. **Vestiture**: stems, pedicels, and calyces glabrous or sparsely to densely hispidulous. **Stems** erect, 5–30 cm tall. **Leaves** herbaceous to semi-succulent, linear-lanceolate, 5–11 mm, sessile, hyphodromous or basal acrodromous, not glandular-punctate, sometimes sparsely hispidulous, margins entire. **Flowers** single, axillary in distal nodes, pedicellate. **Fruiting pedicels** 15–40 mm. **Calyces** semi-succulent, 5–7 mm, lobes shortly deltate-apiculate. **Corollas** yellow or blue with a yellow throat, sometimes red-dotted, tube-throats 4–7 mm, limbs bilabiate, throat open or closed by palate. **Stamens** 4; anthers 2-celled. **Ovaries** 2-locular; **placentation** axile; **stigma** bilamellate. **Fruits** loculicidally dehiscent, thin-walled capsules. **Seed** surface tessellate. **Chromosome number** unknown. **Species** 2. Australia, ?Papua New Guinea, Timor.

1. **Uvedalia linearis** R. Br., Prodr. Fl. Nov. Holland., 440. 1810. *Mimulus linearis* (R. Br.) Wettst., Nat. Pflanzenfam. [Engl. & Prantl] 4(3b): 72. 1891 [non *Mimulus linearis* Benth. 1835]
   M. uvedaliae Benth. in DC., Prodr. 10: 369. 1846.
   a. **Uvedalia linearis** var. **linearis**
      Mimulus uvedaliae var. *uvedaliae*: Benth., Fl. Austral. 4, 482. 1869.
   b. **Uvedalia linearis** var. **lutea** (Benth.) W.R. Barker & Beardsley, **comb. nov.** *Mimulus uvedaliae* var. *lutea* Benth., Fl. Austral. 4, 482. 1869
      M. debilis F. Muell., Trans. Phil. Soc. Vict. 3, 62. 1859.
2. **Uvedalia clementii** (Domin) W.R. Barker & Beardsley, **comb. nov.** *Mimulus clementii*: Bibliot. Bot. Heft 89, 595. 1929.

   The plant tentatively recognized by Beardsley and Barker (2005) as "*Mimulus sp. Pilbara*" (*W.R. Barker 7335*) is identified here as *Uvedalia clementii*.

This group of species has not been distinguished as a genus separate from *Mimulus* for almost 200 years. *Uvedalia*, well-defined on vegetative, floral and seed characters, is under revision by Barker and contains new species, two of which (Beardsley & Barker 2005) he has given informal phrase names: *U. sp. Open papillose throat* (*W.R. Barker 8004*) and *U. sp. Small white flower* (*W.R. Barker 8001*).

V. PEPLIDIUM Delile, Fl. Égypte [Edn. 1]: 148. 1813 [Delile, Descr. Égypte, Hist. Nat. 2: 50. 148. 1813 ("1812"), nomen nudum]. **TYPE**: *Peplidium humifusum* Delile (= *Peplidium maritimum* (L.f.) Asch.), the only species in the protologue.

Terrestrial or semi-aquatic, perennial or annual **herbs**, not rhizomatous. **Vestiture**: glabrous or sparsely to densely eglandular hairy. **Stems** prostrate. **Leaves** semi-succulent, ovate to circular, 3–12 mm, sessile, subsessile or petiolate, the blade floating, fleshy, glandular-punctate, basal or suprabasal acrodromous or hyphodromous. **Flowers** 1–3, axillary in medial to distal nodes, subsessile to pedicellate. **Fruiting pedicels** short to long. **Calyces** tubular, ribbed, ca. 3–5 mm, lobes acute or sub-acute. **Corollas** white to blue-purple, tube-throats cylindric, angled upwards or erect, the limb, the mouth open, sometimes with a palate; limb spreading, prominent, rarely short and suberect, 2-lipped or sub-actinomorphic. **Stamens** 4 or 2, anthers 1-celled. **Ovaries** 2-locular; **placentation** axile; **stigma** unilamellate, through reduction of adaxial lobe to a vestige, usually irritable, covering the front of the corolla tube. **Fruits** bilocular, loculicidally dehiscent or tardily dehiscent capsules. **Seed** surface reticulate or thick-ribbed, the ribs with a row of areolae on each side, sometimes some ribs wing-like. **Chromosome number** unknown. **Species** 4. Mostly subtropical, arid and semi-arid Australia, with *P. maritimum* extending to North Africa, India.

1. **Peplidium aithocheilum** W.R. Barker, J. Adel. Bot. Gard. 13: 88. 1990
2. **Peplidium foecundum** W.R. Barker, J. Adel. Bot. Gard. 15: 71. 1992
3. **Peplidium maritimum** (L.f.) Asch., Beitrag. Fl. Aethiop: 275. 306. 1867. *Hedyotis maritima* L.f., Suppl. Pl: 119. 1781[1782].
   P. humifusum Delile, Fl. Egypte [Edn. 1]: 148. 1813; [Delile, Descr. Egypte, Hist. Nat. 50. 1813 ("1812"), nomen nudum].
4. **Peplidium muelleri** Benth., Fl. Austral. 4: 500. 1868

Peplidium shares with *Microcarpaea* and *Glossostigma* single-celled anthers and a unilamellate stigma derived by the reduction of the adaxial lamella to a small vestige. The single lamella is generally irritable except in the very small flowered species which from the low pollen-ovule ratios are apparently obligately autogamous (Barker 1982). Revisional studies (Barker in prep.) indicate at least 14 species, with a number of phrase names designated by Barker for interim use (Beardsley & Barker 2005): *P. sp. Tanami* (*W.R. Barker 2819*), *P. sp. Yelma* (*R.J. Chinnock 4620*), *P. sp. Harding Dam* (*W.R. Barker 7357*), *P. sp. Marla* (*W.R. Barker 3535*), *P. sp. Banjawarn* (*R..J. Chinnock 745*), *P. sp. Pilbara W.R. Barker 7285*), *P. sp. Recurved limb* (*W.R. Barker 7246*) and *P. sp. Closed lips* (*W.R. Barker 7324*).

VI. ELACHOLOMA F. Muell. & Tate ex F. Muell., Vict. Naturalist 12: 14. May 1895 [F. Muell. & Tate ex Tate, Trans. Roy. Soc. S. Austral. 19: 79. July 1895, nomen nudum]. **TYPE**: *Elacholoma hornii* F. Muell. & Tate, the only species in the protologue.

Terrestrial or semi-aquatic, annual **herbs**, not rhizomatous. **Vestiture**: leaves sparsely to densely minutely scabrous-hispidulous to hispid with eglandular hairs along the margins or all over. **Stems** prostrate. **Leaves** semi-succulent, linear-oblong to linear-oblanceolate, 3–12 mm, sessile, not glandular-punctate, hyphodromous. **Flowers** single, axillary at medial to distal nodes, subsessile to pedicellate. **Fruiting pedicels** to ca. 10–15 mm long. **Calyces** tubular, 1–3 mm., ribbed, lobes

deltoid. **Corollas** white or blue-purple, tube-throats cylindric, limb expanded or not. **Stamens** 4 or 2; anthers with 2 confluent cells. **Ovaries** 2-locular; **placentation** axile; **stigma** bilobed, the lobes lamellate or filiform. **Fruits** bilocular, loculicidally dehiscent capsules. **Seed** surface reticulate. **Chromosome number** unknown. **Species** 2. Arid Australia.

1. **Elacholoma hornii** F. Muell. & Tate, Vict. Naturalist 12: 14. 1895.
2. **Elacholoma prostrata** (Benth.) W.R. Barker & Beardsley, **comb. nov.** *Mimulus prostratus* Benth. in DC., Prodr. 10: 373. 1846.
   M. pusillus Benth. in DC., Prodr. 10: 369. 1846.

The genus also contains an undescribed species. *Elacholoma sp. Showy flowers* (*C.P. Campbell 1762*) (fide Beardsley & Barker 2005) will be formally described by W.R. Barker and M. Hislop now that generic placement is finalized.

The flowers of this genus furnish synapomporphies, notably the actinomorphic corolla and a forward-directed bilobed stigma centrally positioned in the corolla. *Elacholoma prostrata* retains the bilamellate stigma of *Mimulus* sensu stricto, *Thyridia*, and the American-Asian clade, but *E. hornii* and *E. sp. Showy flowers* differ by their filiform exserted stigmas, which are unique in Phrymaceae and across families now segregated from the traditional Scrophulariaceae. This presumably reflects a shift to lepidopteran pollination evident also in the long corolla tube in the latter species. These two species are better combined as a single monophyletic genus, emphasizing their close monophyletic relationship (Beardsley & Barker 2005).

VII. GLOSSOSTIGMA Wight & Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 355. 1836, nom. cons. **TYPE**: *Glossostigma spathulatum* Arn., nom. illeg. (*Limosella diandra* L. = *Glossostigma diandrum* (L.) Kuntze), the only species in the protologue.
Tricholoma Benth. in DC., Prodr. 10: 426. 1846, nom. rejic. **TYPE**: *T. elatinoides* Benth. = *G. elatinoides* (Benth.) Benth. ex J.D. Hook., non *Tricholoma* (Fr.) Staude, nom. cons. (Fungi: Agaricaceae), the only species in the protologue.

Semi-aquatic or aquatic small to tiny, annual **herbs**, sometimes rhizomatous, sometimes forming mats. **Vestiture**: glabrous. **Stems** repent, on wet mud, often rooting at nodes. **Leaves** linear-oblong to spatulate, blades obovate to elliptic, fleshy, 2–8 mm, not glandular-punctate, hyphodromous, margins entire, base attentuate to subpetiolate. **Flowers** single, axillary, in medial to distal nodes, subsessile to pedicellate. **Fruiting pedicels** 0 to ca. 100 mm long. **Calyces** 1–2.5 mm, zygomorphic, not ribbed or winged, lobes 3–4, unequal, obutse. **Corollas** white or blue- or red-purple, with a white or yellow mouth, tube-throats 1–1.5 mm, stamens inserted near mouth, limb 2-lipped or sub-rotate. **Stamens** 4 or 2, 1-celled. **Ovaries** 2-locular, **placentation** axile; **stigma** unilamellate through adaxial lobe reduced to vestige, usually irritable. **Fruits** bilocular, loculicidally dehiscent capsules, sometimes (*G. cleistanthum*) when plant aquatic thick-walled and indehiscent, becoming thin on drying of substrate. **Seed** surface reticulate. **Chromosome number** unknown. **Species** 5. Mainly Australia and New Zealand, with *G. diandrum* extended into India, Indochina, and apparently southern Africa (though it is only known from the type of *G. diandrum* purported to come from the Cape of Good Hope), and since 1992 recorded as naturalized in eastern North America (e.g., Les et al. 2006; *G. cleistanthum*).

1. **Glossostigma cleistanthum** W.R. Barker, J.Adel. Bot. Gard. 15: 72. 1992.
2. **Glossostigma diandrum** (L.) Kuntze, Rev. Gen. Plant. 1: 461. 1891. *Limosella diandrum* L., Mant. Plant. 1: 252. 1767.
   G. submersum Petrie, Trans. & Proc. N. Zeal. Inst. 23: 401. 1891.
3. **Glossostgma drummondii** Benth. in DC., Prodr. 10: 426. 1846. *Limosella drummondii* (Benth.) F. Muell., Fragm. Phyt. Austral. 6: 104 1868

4. Glossostigma elatinoides (Benth.) Benth. ex J.D. Hook., Bot. Antarct. Voy. II. (Fl. Nov.-Zel.) 189. 1853. *Tricholoma elatinoides* Benth. in DC., Prodr. 10: 426. 1846.
5. Glossostigma trichodes F. Muell., Vict. Nat. 9: 128. 1893.

Revisionary studies (Barker in prep.) define at least eight species, with two given phrase names: *G. sp. Large flowered* (*W.R. Barker* 7277) and *G. Long stout pedicelled* (*W.R. Barker 2481*) (cf. Beardsley & Barker 2005).

VIII. **PHRYMA** L., Sp. Pl. 2: 601. 1753. *Leptostachia* Adans., Fam. 2: 201. 1763 (superfluous replacement name for *Phryma* L.). **TYPE**: *Phryma leptostachya* L., the sole species in the protologue.

Perennial, rhizomatous, terrestrial. **Vestiture**: glabrous to minutely puberulent, eglandular. **Stems** herbaceous, erect, 4-angled. **Leaves** petiolate, herbaceous, not glandular-punctate venation brochidodromous. **Flowers** ca. 20–40, subopposite, sessile to subsessile in terminal and axillary spikes, bracts and bracteoles greatly reduced and inconspicuous. **Fruiting pedicels** absent or nearly so. **Fruiting calyces** strongly reflexed and appressed to the inflorescence axis, tube midveins ribbed. **Corollas** white to pinkish or reddish to violet, tardily marcescent, limbs bilabiate. **Stamens** 4, anthers 2-celled. **Ovaries** 1-locular (pseudomonomerous, 2-carpellate with 1 carpel reduced developmentally); **placentation** basal; **stigmas** bilamellate. **Fruits** 1-seeded achenes, enclosed in persistent calyx, unilocular, indehiscent. **Seed** surface not evident (the integument breaks down during fruit maturation, finally reduced to a cuticular layer within the mature fruit). **Chromosome number**, $2n = 28$. **Species** 1.

Whipple (1972) has a brief summary of the classification history of *Phryma*. It was first segregated at the rank of family by Schauer (1847), who emphasized the distinctive gynoecial features in distinguishing it from Verbenaceae. Fruit development suggested to Whipple that the uniovulate, uniloculate gynoecium is derived from a similar fruit type found in Verbenaceae-Lantaneae — as in *Phryma*, the abaxial carpel is suppressed in *Lantana*, *Lippia*, and *Stachytarpheta*. She also observed that floral vascularization in *Phryma* and these three genera is basically alike.

(FNANM, ASIA)
1. Phryma leptostachya L., Sp. Pl. 601. 1753.
Phryma leptostachya var. *asiatica* H. Hara, Enum. Spermatoph. Jap. 1: 297. 1948. *Phryma leptostachya* subsp. *asiatica* (H. Hara) Kitam., Acta Phytotax. Geobot. 17: 7. 1957. *Phryma asiatica* (H. Hara) O. Deg. & I. Deg., Phytologia 22: 212. 1971.

Phryma includes populations disjunct between eastern North America and southeastern Asia. These have been variously treated as two races, varieties, or separate species (Thieret 1972; Whipple 1972; Lee et al. 1996; Cantino 2004; Deyuan & Wen 2011). The disjunct plants show distinct molecular divergence but no morpho-geographic groups at the intercontinental level (Nie et al. 2006).

IX. **HEMICHAENA** Benth., Pl. Hartw., 78. 1841. **TYPE**: *Hemichaena fruticosa* Benth. (= *Mimulus fruticosus*).
Mimulus sect. *Tropanthus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 324. 1925 ("1924"). **TYPE**: *Mimulus treleasei* A.L. Grant (= *Mimulus levigatus*), the only species in the protologue.
Berendtia A. Gray, Proc. Amer. Acad. Arts 7: 379. 1868 (non Goeppert 1845). *Berendtiella* Wettst. & Harms in Engl. & Prantl, Pflanzenfam. II.-IV: 459. 1899. [a replacement name for *Berendtia* A. Gray]. **LECTOTYPE** (Thieret 1972b, p. 92): *Berendtia ghiesbrechtii* A. Gray (= *Mimulus rugosus*). Gray did not cite a type for his new genus, in which he included *B. ghiesbrechtii*, *B. coulteri*, and *B. rugosa*.

Plants perennial, rhizomatous or woody-taprooted. **Vestiture**: viscid-pilose or glabrous. **Stems** woody, terete, erect or prostrate-creeping, terete. **Leaves** petiolate, herbaceous, not glandular-punctate, venation eucamptodromous. **Flowers** 1–5(–12) in bracteolate axillary cymes. **Fruiting pedicels** shorter to about equal or slightly longer than the calyces. **Fruiting calyces** erect, low-plicate. **Corollas** red or yellow, marcescent, limbs bilabiate. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** parietal; **stigmas** bilamellate. **Fruits** many-seeded capsules with rounded apices, stipitate-glandular, loosely enclosed in persistent calyx, included, bilocular, loculicidally dehiscent along both sutures to the base. **Seed** surface tesselate. **Chromosome number** unknown. **Species** 5.

(MEXICO, CENTRAL AMERICA)

1. **Hemichaena coulteri** (A. Gray) Thieret, Fieldiana, Bot. 34: 94. 1972. *Berendtia coulteri* A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868. *Berendtiella coulteri* (A. Gray) Thieret, Ceiba 4: 305. 1955. *Mimulus coulteri* (A. Gray) G.L. Nesom, Phytoneuron 2011-28: 7. 2011.
2. **Hemichaena fruticosa** Benth., Pl. Hartw., 78. 1841. *Leucocarpus fruticosus* (Benth.) Benth. in DC., Prodr. 10: 336. 1846. *Mimulus fruticosus* (Benth.) G.L. Nesom, Phytoneuron 2011-28: 5. 2011.
3. **Hemichaena levigata** (B.L. Rob. & Greenm.) Thieret, Fieldiana, Bot. 34: 96. 1972. *Berendtia levigata* B.L.Rob. & Greenm., Proc. Amer. Acad. Arts 32: 39. 1897. *Berendtiella levigata* (B.L.Rob. & Greenm.) Thieret, Ceiba 4: 305. 1955. *Mimulus levigatus* (B.L. Rob. & Greenm.) G.L. Nesom, Phytoneuron 2011-28: 6. 2011.
   Mimulus treleasei A.L. Grant, Ann. Missouri Bot. Gard. 11: 325. 1925 ("1924").
4. **Hemichaena spinulosa** (S. Watson) Thieret, Fieldiana, Bot. 34: 98. 1972. *Berendtia spinulosa* S. Watson, Proc. Amer. Acad. Arts 25: 159. 1890. *Berendtiella spinulosa* (S. Watson) Thieret, Ceiba 4: 305. 1955. *Mimulus spinulosus* (S. Watson) G.L. Nesom, Phytoneuron 2011-28: 6. 2011.
5. **Hemichaena rugosa** (Benth.) Thieret, Fieldiana, Bot. 34: 96. 1972. *Diplacus rugosus* Benth. in DC., Prodr. 10: 368. 1846. *Berendtia rugosa* (Benth.) A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868. *Berendtiella rugosa* (Benth.) Thieret, Ceiba 4: 305. 1955. *Mimulus rugosus* (Benth.) G.L. Nesom, Phytoneuron 2011-28: 7. 2011.

In uniting the 5 species of *Berendtiella* and *Hemichaena* (all as *Hemichaena*), Thieret (1972b, p. 89) observed that "The genera *Leucocarpus*, *Berendtiella*, and *Hemichaena* possess floral characteristics that indicate their alliance with *Mimulus* and so have been transferred to the Gratioleae. These three genera are rather similar in certain vegetative features and in inflorescence, suggesting close affinity." *Leucocarpus* and *Hemichaena* were formally brought into *Mimulus* (Nesom 2011) with the intent of using *Mimulus* as the name for the western North American and Central American species, an idea relinquished here.

The woody-stemmed, shrubby habit of *Hemichaena* has developed in parallel in *Diplacus* sect. *Diplacus*, and the mix of red and yellow corolla colors also is encountered within other sections of *Diplacus*. The axillary cymoid inflorescences of *Hemichaena* also are produced by *Leucocarpus perfoliatus*. In the context of the phylogeny shown in Figure 1, these complex structures are hypothesized to be specialized and developed in parallel within Phrymaceae.

X. **MIMETANTHE** Greene, Bull. Calif. Acad. Sci. 1: 181. 1886[1885]. **TYPE**: *Mimetanthe pilosa* (Benth.) Greene

Herpestis sect. *Mimuloides* Benth. in DC., Prodr. 10: 394. 1846. *Mimulus* § *Mimuloides* (Benth.) Benth. & J.D. Hook., Gen. Pl. 2(2): 947. 1876. **TYPE**: *Herpestis pilosa* Benth. [= *Mimetanthe pilosa*] Watson (1871) noted that the species had been recognized as *Herpestis* sect. *Mimuloides* but he did not formally transfer the section to *Mimulus*.

Annual, fibrous-rooted or taprooted, terrestrial. **Vestiture**: stems, leaves, and calyces prominently glandular-villous. **Stems** herbaceous, terete, erect. **Leaves** sessile, herbaceous, not

glandular-punctate 1-veined (hyphodromous) or weakly 3-veined (basal acrodromous). **Flowers** single, axillary, usually racemose. **Fruiting pedicels** about equal to the calyces in length or slightly longer. **Fruiting calyces** erect, becoming swollen-ovoid in fruit, midveins low-rounded (not angled or winged), lobes strongly unequal **Corollas** yellow with 2 purple spots on ventral lip, marcescent to quickly deciduous, limbs slightly to strongly bilabiate. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** parietal; **stigmas** bilamellate. **Fruits** many-seeded capsules with attenuate apices, minutely and densely pustulate-glandular, loosely enclosed in persistent calyx, included or slightly exserted, bilocular, loculicidally dehiscent along the distal 1/3–1/2 of both sutures, placentae fused and also remaining attached to the walls or sometimes dividing in the distal 1/3–1/2, both valves in dehiscence spreading-reflexing in so far as separated. **Seed** surface reticulate, minutely glandular. **Chromosome number** apparently unknown. **Species** 1.

(FNANM, MEXICO)

1. Mimetanthe pilosa (Benth.) Greene, Bull. Calif. Acad. Sci. 1: 181. 1885. *Herpestis pilosa* Benth., Companion Bot. Mag. 2: 57. 1836. *Mimulus pilosus* (Benth.) S. Watson, Bot. 40th Parallel, 225. 1871. *Mimulus exilis* Durand & Hilg., Pl. Heermannianae 43. 1854 [Nov 1854] ; J. Acad. Nat. Sci. Philadelphia, n.s., 3: 43. May 1855

This species has been segregated in the past as the monotypic genus *Mimetanthe* Greene and has been treated as such by Grant (1924) and other botanists (e.g., Holmgren 1984) but not by Pennell (1951), Munz (1959), or Thompson (1993, 2005). Bentham originally described *Mimulus pilosus* in the genus *Herpestis* Gaertn. (1807), but *Herpestis* is now regarded as a synonym of *Bacopa* Aubl.

Parietal placentation and apically attenuate fruits without prismatic or angled walls are synapomorphic within *Diplacus*. As a result the species could justifiably be included within *Diplacus* as sister to the rest of the genus. The decision to maintain it as a separate genus is subjective, but the species has unique specializations in pollen morphology (Argue 1980, 1984) and floral morphology that have been emphasized by previous botanists; the fusion of its parietal placentae is another specialization apparently not encountered in any species of *Diplacus*. Gray (1886, p. 279) noted this: "Annual, with corolla of *Eumimulus*, capsule with the divided placentae of *Eunanus*, but the calyx campanulate and 5-cleft; its tube not prismatic nor even carinate-angled, but almost nerveless; its lobes plane."

Greene (1885, p. 122) included the species within *Mimulus*, describing it thus: "A soft-hairy, pale-green, Californian annual, uniting the characters partly of *Herpestis* and partly of *Eunanus*, with a habit which is not that of either of those genera, nor yet of *Mimulus*. Very likely it were better disposed of as a generic type, as was long ago suggested, but not carried into effect, by Durand & Hilgard." Very shortly thereafter, Greene (1885) formally segregated it as *Mimetanthe*, with these comments (p. 181): "The peculiar dehiscence, with the singular bending back of the valves, will hardly be observable in herbarium specimens, which are almost always too young to show it; but in autumn or midwinter, when the foliage and calyces are decayed, and the capsules alone persist upon the dead stems and branches, this character becomes conspicuous."

The isolated taxonomic position of this species is recognized here but it is clear that further morphological and molecular work needs to be done to confirm its sister relationship to *Diplacus*. The current position is not supported based on the analysis presented in Beadsley et al. (2004, Fig. 1).

XI. DIPLACUS Nutt., Ann. Nat. Hist. 1: 137. 1838. *Mimulus* [unranked] *Diplacus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876 [*Mimulus* sect. *Diplacus* (Nutt.) Benth. & J.D. Hook., Gen. Pl. 2(2): 947. 1876]. **LECTOTYPE** (Thompson 2005): *Diplacus glutinosus* (J.C.Wendl.) Nutt. [= *Diplacus aurantiacus*].

Mimulus subg. *Schizoplacus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924"). **LECTOTYPE**: (Thompson 2005, p. 26): *Mimulus nanus* Hook. & Arn. [= *Diplacus nanus*].

Annual (fibrous-rooted or slender taprooted) or **perennial** (taprooted or, in one species, rhizomatous), terrestrial. **Vestiture**: puberulent-glandular to villous-glandular or puberulent to softly hirsute or villous and non-glandular, less commonly glabrous. **Stems** herbaceous or woody, erect, terete. **Leaves** petiolate or sessile, herbaceous, not glandular-punctate, venation acrodromous (suprabasal basal) to hyphodromous. **Flowers** single, axillary, often appearing sessile from the basal rosette because of foreshortened nodes. **Fruiting pedicels** absent or at least usually distinctly shorter than the calyx. **Fruiting calyces** erect, tube midveins plicate-raised or angle- to rounded-ridged. **Corollas** yellow, white, white with purple patterning, pink, purple to light violet, red, orange, marcescent (sometimes deciduous in *D. pictus* and *D. mohavensis*), limbs bilabiate to regular. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** parietal; **stigmas** bilamellate. **Fruits** many-seeded capsules with attenuate apices, glabrous, loosely enclosed in persistent calyx, often slightly exserted, bilocular, loculicidally dehiscent (initially indehiscent in sect. *Oenoe*) along the distal half of the inner (upper) suture to only distally along the outer (lower) suture. **Seed** surface reticulate to nearly smooth. **Chromosome numbers** $2n$ = 16, 18, 20. **Species** 46.

The attenuate tips of the capsule valves are usually exserted from the calyx and often form a chute-like passage for the seeds during dispersal. In sect. *Oenoe*, the initially indehiscent fruits open along the inner suture after being wet by fall or winter rains, long after senescence.

1. **DIPLACUS** sect. **EREMIMIMULUS** G.L. Nesom & N.S. Fraga, **sect. nov.** **TYPE**: *Diplacus parryi* (A. Gray) G.L. Nesom & N.S. Fraga

Annual (*D. parryi*) or perennial (*D. rupicola*), puberulent to softly hirsute, glandular; leaves mostly basal or near-basal on short stems, blades narrowly lanceolate to lanceolate or oblanceolate, pinnately to subpinnately veined; flowers usually 2 per node; pedicels usually shorter than calyces, sometimes nearly subequal; corollas rotate and nearly radial, persistent, lobes whitish to pink (*D. rupicola*) or purple to yellow (*D. parryi*) with yellow ventral ridges; anthers glabrous; styles glandular pubescent, stigma lobes equal; fruits dehiscent (tardily in *D. rupicola*). x = 8.

(FNANM)

1. **Diplacus parryi** (A. Gray) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus parryi* A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876.
2. **Diplacus rupicola** (Coville & A.L. Grant) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus rupicola* Coville & A.L. Grant, J. Wash. Acad. Sci. 26: 99. 1936.

Diplacus rupicola is endemic to Inyo County, California; *D. parryi* also occurs there as well as in nearby regions of Nevada, Utah, and Arizona.

These two species are placed as sister species (100% bootstrap confidence) in the molecular analysis by Beardsley et al. (2004) and very weakly supported as sister to the rest of the genus *Diplacus* (Fig. 1). They differ in a number of striking features, as in the couplet below, but both are species of Mojave Desert habitats and both have unequal stigma lobes, 2-flowered nodes, and a base chromosome number of x = 8. Unequal stigma lobes and 2-flowered nodes occur in other species of *Diplacus* and x = 8 apparently is plesiomorphic, but their association in these two species may indicate a degree of genetic coherence.

1. Annual; hypocotyls epigeous; capsules with fragile walls, promptly dehiscent; corolla lobes without a large spot at the base; seeds ca. 20–30, 0.5–0.8 mm long ..... **Diplacus parryi**
1. Perennial; hypocotyls hypogeous; capsules with indurate walls, dehiscent after senescence of stem; corolla lobes with a large spot at the base; seeds 3–10, 1.2–1.5 mm long ..... **Diplacus rupicola**

Because of its indurate capsule walls and hypogeous hypocotyls, *Diplacus rupicola* was included by Thompson (2005) in sect. *Oenoe* (among the species treated here as sect. *Cleisanthus*), but those species have 1-flowered nodes and a base chromosome number of x = 9. *Diplacus parryi* was included in sect. *Eunanus* because of its 2-flowered nodes and fragile-walled, promptly dehiscent capsules.

Treatment here of *Diplacus rupicola* and *D. parryi* as sister species weights the molecular data. Additional sequence data, however, or further morphological study presumably might support the positioning of *D. parryi* in sect. *Eunanus* (or at least not contradict it), leaving *Erimimimulus* as a monotypic section. Alternatively, unequivocal synapomorphies might be found to link the two. The hypothesis of close relationship tentatively adopted here appeals to further study. The name of the section (from Greek, *eremos*, desert, solitude) alludes to the habitat of the species and to their juxtaposed-but-isolated taxonomic position.

2. DIPLACUS sect. **EUNANUS** (Benth.) G.L. Nesom & N.S. Fraga, **comb. nov.** *Eunanus* Benth. in DC., Prodr. 10: 374. 1846. *Mimulus* § *Eunanus* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876. **LECTOTYPE** (Thompson 2005): *Eunanus tolmiei* Benth. [= *Diplacus nanus* (Hook. & Arn.) G.L. Nesom & N.S. Fraga]

Mimulus sect. *Mimulastrum* A. Gray in Lemmon, Bot. Gaz. (Crawfordsville) 9: 141. 1884. *Eunanus* § *Mimulastrum* (A. Gray) Greene, Bull. Calif. Acad. Sci. 1: 105. 1885. **TYPE**: *Mimulus mohavensis* Lemmon. Gray (in Lemmon) included only *M. mohavensis* in the new section. See comments below under sect. *Pseudonoe*.

Annual, puberulent-glandular; leaf blades narrowly elliptic, lanceolate, oblanceolate or oblong-obovate; flowers 1 per node (*D. fremontii*, *D. rattanii*, *D. viscidus*) or 2 per node; corollas yellow (*D. brevipes*, *D. whitneyi*, *D. mephiticus*) or purple to light violet, bilabiate, persistent, throat not strongly developed; styles glandular-pubescent; stigma lobes subequal to unequal; capsules fragile, symmetric at base, usually promptly dehiscent along both sutures distally (if not promptly dehiscent then straight and nearly fusiform). x = 8.

(FNANM)

1a. **Diplacus bigelovii** (A. Gray) G.L. Nesom, **comb. nov.** *Eunanus bigelovii* A. Gray, Pacif., Railr. Rep. 4(5): 121. 1857. *Mimulus bigelovii* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 11: 96. 1876.

1b. **Diplacus bigelovii** var. **cuspidatus** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus bigelovii* var. *cuspidatus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 279. 1924 ["1924"].
Mimulus spissus A.L. Grant, Ann. Missouri Bot. Gard. 11: 277. 1924 ["1924"].

2. **Diplacus bolanderi** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus bolanderi* A. Gray, Proc. Amer. Acad. Arts 7: 381. 1868. *Eunanus bolanderi* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 105. 1885.

3. **Diplacus brevipes** (Benth.) G.L. Nesom, **comb. nov.** *Mimulus brevipes* Benth., Scroph. Ind. 28. 1835. *Eunanus brevipes* (Benth.) Greene, Bull. Calif. Acad. Sci 1: 105. 1885.

4. **Diplacus clivicola** (Greenm.) G.L. Nesom, **comb. nov.** *Mimulus clivicola* Greenm., Erythea 7: 119. 1899. *Eunanus clivicola* (Greenm.) A. Heller, Muhlenbergia 1: 60. 1904.

5. **Diplacus compactus** (D.M. Thompson) G.L. Nesom, Phytoneuron 2012-47: 1. 2012. *Mimulus viscidus* var. *compactus* D.M. Thompson, Syst. Bot. Monogr. 75: 129. 2005.

6. **Diplacus constrictus** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus subsecundus* subsp. *constrictus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 287. 1925 ("1924"). *Mimulus constrictus* (A.L. Grant) Pennell, Illustr. Fl. Pacific States 3: 722. 1951. *Mimulus viscidus* subsp. *constrictus* (A.L. Grant) Munz, Aliso 4: 99. 1958.

7. **Diplacus cusickii** (Greene) G.L. Nesom, **comb. nov.** *Eunanus cusickii* Greene, Pittonia 1: 36. 1887. *Mimulus cusickii* (Greene) Rattan, Analytical Key West Coast Bot. (ed. 3) 63. 1898.

8. **Diplacus fremontii** (Benth.) G.L. Nesom, **comb. nov.** *Eunanus fremontii* Benth. in DC., Prodr. 10: 374. 1846. *Mimulus fremontii* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 96. 1876.

Mimulus subsecundus A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 445. 1886. *Eunanus subsecundus* (A. Gray) Greene, Pittonia 1: 37. 1887.

9. **Diplacus jepsonii** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus jepsonii* A.L. Grant, Ann. Missouri Bot. Gard. 11: 306. 1925 ("1924").
10. **Diplacus johnstonii** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus johnstonii* A.L. Grant, Ann. Missouri Bot. Gard. 11: 280. 1925 ("1924").
11. **Diplacus layneae** (Greene) G.L. Nesom, **comb. nov.** *Eunanus layneae* Greene, Bull. Calif. Acad. Sci. 1: 104. 1885. *Mimulus layneae* (Greene) Jeps., Fl. W. Calif. 405. 1901.
12. **Diplacus leptaleus** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus leptaleus* A. Gray, Proc. Amer. Acad. Arts 11: 96. 1876. *Eunanus leptaleus* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 101. 1885.
13. **Diplacus mephiticus** (Greene) G.L. Nesom, **comb. nov.** *Mimulus mephiticus* Greene, Bull. Calif. Acad. Sci. 1: 9. 1884. *Eunanus mephiticus* (Greene) Greene, Bull. Calif. Acad. Sci 1: 102. 1885.
    Mimulus coccineus Congdon, Erythea 7: 187. 1900.
    Mimulus angustifolius (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 298. 1925 ("1924").
    Mimulus densus A.L. Grant, Ann. Missouri Bot. Gard. 11: 298. 1925 ("1924").
14. **Diplacus mohavensis** (Lemmon) G.L. Nesom, **comb. nov.** *Mimulus mohavensis* Lemmon, Bot. Gaz. 9: 142. 1884. *Eunanus mohavensis* (Lemmon) Greene, Bull. Calif. Acad. Sci 1: 106. 1885.

    Diplacus mohavensis is similar to *D. pictus* in features of corolla morphology and color patterning, and the pair sometimes has been segregated as a ditypic *Mimulus* sect. *Mimulastrum* (e.g., Thompson 2005). Molecular data, however, indicate that *D. mohavensis* arose from within sect. *Eunanus*. It is distinct from other species of the section (and similar to *D. pictus*) in its radially symmetric, salverform-rotate corollas with an abrupt tube-throat transition and vein-patterned limb. In *D. mohavensis*, the limb is purplish brown basally with red, irregularly patterned veins fading into a wide, whitish distal border; in *D. pictus*, the limb is all white and the vein patterning is more regular and not fading distally.
15. **Diplacus nanus** (Hook. & Arn.) G.L. Nesom, **comb. nov.** *Mimulus nanus* Hook. & Arn., Bot. Beechey Voy. 378. 1839. *Eunanus nanus* (Hook. & Arn.) Holz., Contr. U.S. Natl. Herb. 3: 244. 1895. *Eunanus tolmiei* Benth. in DC. Prodr was the name used by Bentham. and Greene for this sp; Grant treated it as a syn. Bentham. and Green spelled it *tolmiaei*, but Bentham cited the collector as Tolmie.

    In the molecular phylogeny by Beardsley et al. (2004), samples of *Diplacus nanus* are placed in three disparate positions within the cladistic topology of the section.
16. **Diplacus ovatus** (A. Gray) G.L. Nesom, Phytoneuron 2012-47: 3. 2012. *Mimulus bigelovii* A. Gray var. *ovatus* A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 445. 1886. *Mimulus ovatus* (A. Gray) N.H. Holmgren, Intermount. Fl. 4: 362. 1984.
17. **Diplacus rattanii** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus rattanii* A. Gray, Proc. Amer. Acad. Arts 20: 307. 1885. *Eunanus rattanii* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 105. 1885.
    Mimulus decurtatus A.L. Grant, Ann. Missouri Bot. Gard. 11: 288. 1925 ("1924"). *Mimulus rattanii* var. *decurtatus* (A.L. Grant) Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia 236: 1. 1951.
18. **Diplacus vandenbergensis** (D.M. Thomps.) G.L. Nesom, Phytoneuron 2012-47: 2. 2012. *Mimulus fremontii* var. *vandenbergensis* D.M. Thomps., Syst. Bot. Monogr. 75: 134. 2005.
19. **Diplacus viscidus** (Congdon) G.L. Nesom, **comb. nov.** *Mimulus viscidus* Congdon, Erythea 7: 187. 1900. *Mimulus fremontii* var. *viscidus* (Congdon) Jeps, Man. Fl. Pl. Calif. 924. 1925. *Mimulus subsecundus* var. *viscidus* (Congdon) A.L. Grant, Ann. Missouri Bot. Gard. 11: 286. 1925 ("1924").
20. **Diplacus whitneyi** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus whitneyi* A. Gray, Syn. Fl. N. Amer. 2(1, Suppl.): 445. 1886.
    Eunanus bicolor A. Gray, Proc. Amer. Acad. Arts 7: 381. 1868. *Mimulus nanus* var. *bicolor* (A. Gray) A. Gray, Bot. California 1: 564. 1876.

The status of some of these taxa, including synonyms, is discussed by Nesom (2012f).

3. DIPLACUS sect. **PSEUDOENOE** (A.L. Grant) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* sect. *Pseudoenoe* A.L. Grant, Ann. Missouri Bot. Gard. 11: 323. 1925 ["1924"]. **TYPE**: *Mimulus pictus* (Curran ex Greene) A. Gray [= *Diplacus pictus*]. Gray (in Lemmon 1884) included only *M. mohavensis* in sect. *Mimulastrum* but Greene (1885) added *M. pictus* (as *Eunanus pictus*) to the section, and Gray (1886) also included both species in sect. *Mimulastrum*. With

Grant's (1924) creation of sect. *Pseudoenoe* for *M. pictus*, each species thus constituted a monotypic section in her treatment.

Annual; pedicels shorter than calyces; corollas radially symmetric, salverform, throat not strongly developed, lobes white with an intricate weblike purple- or burgundy-veined pattern; lower stigma lobe 6–8 times longer than upper; styles glandular pubescent; flowers sometimes cleistogamous. x = 8.

(FNANM)

1. **Diplacus pictus** (Curran ex Greene) G.L. Nesom, **comb. nov.** *Eunanus pictus* Curran ex Greene, Bull. Calif. Acad. Sci. 1: 106. 1885. *Mimulus pictus* (Curran ex Greene) A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1, Suppl.): 446. 1886.

On occasions *Diplacus pictus* and *D. mohavensis* have been treated together as *Mimulus* sect. *Mimulastrum* (A. Gray) Wettst. (*M. mohavensis* the type) (e.g., Wettstein 1891, Thompson 2005). Grant (1924) separated them as monotypic sections. Despite their remarkable similarity in corolla morphology and color patterning, molecular data show *D. mohavensis* to be separately derived from within sect. *Eunanus*. Argue (1980) found that *D. pictus* has microreticulate tricolpate pollen grains while those of *D. mohavensis* are perforate tricolpate.

4. **DIPLACUS** sect. **OENOE** (A. Gray) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* § *Oenoe* A. Gray in W.H. Brewer, S. Watson, and A. Gray, Bot. California (ed. 1): 563. 1876. *Eunanus* sect. *Oenoe* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 98. 1885. **LECTOTYPE** (Thompson 2005): *Mimulus tricolor* Hartweg ex Lindley [= *Diplacus tricolor*] Bentham (Pl. Hartw. 329. 1849) appears to suggest that, instead of within *Eunanus*, *Eunanus douglasii* would be better considered within Gray's genus *Oenoe*, but in 1849 the name *Oenoe* had not yet been published at any rank.

Mimulus sect. *Microphyton* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 170. 1947. **TYPE**: *Mimulus pygmaeus* A.L. Grant, the only species included in the protologue.

Annual, pedicels shorter than calyces; glandular-puberulent or (*D. angustatus*) villous-nonglandular; leaves narrowly lanceolate to oblanceolate; corollas yellow (*D. pygmaeus*) or bicolored to tricolored, bilabiate to subbilabiate, broadly funnelform-rotate, tube-throats narrowly cylindric, much longer than the calyx to barely longer, persistent; anthers hairy; styles glandular-pubescent; capsules indurate, often basally asymmetric, indehiscent. x = 9, 10.

(FNANM)

1. **Diplacus angustatus** (A. Gray) G.L. Nesom, **comb. nov.** *Eunanus coulteri* Harvey & A. Gray ex Bentham var. *angustatus* A. Gray, Proc. Amer. Acad. Arts 7: 381. 1868. *Mimulus tricolor* var. *angustatus* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876. *Eunanus angustatus* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 99. 1885. *Mimulus angustatus* (A. Gray) A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1, Suppl.): 443. 1886.
2. **Diplacus pulchellus** (Drew ex Greene) G.L. Nesom, **comb. nov.** *Eunanus pulchellus* Drew ex Greene, Pittonia 2: 104. 1890. *Mimulus pulchellus* (Drew ex Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 316. 1925 ("1924").
3. **Diplacus pygmaeus** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus pygmaeus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 312. 1925 ("1924").
4. **Diplacus tricolor** (Hartweg ex Lindl.) G.L. Nesom, **comb. nov.** *Mimulus tricolor* Hartweg ex Lindl., J. Hort. Soc. London 4: 222. 1849. *Eunanus tricolor* (Hartweg ex Lindl.) Greene, Bull. Calif. Acad. Sci 1: 99. 1885.

Eunanus coulteri Harvey & A. Gray ex Benth., Pl. Hartw., 329. 1849.

Thompson (2005, p. 29) noted that this group of species is characterized by subequal stigma lobes, linear cotyledons, hypogeous hypocotyls, and one flower per node and that they are restricted in habitat to vernally wet depressions or seepages (contrast with sect. *Cleisanthus*). Thompson (2005) included all ten species with indehiscent fruits in sect. *Oenoe* — these are divided here among sects. *Oenoe* and *Cleisanthus*. "The indehiscent fruits of sect. *Oenoe* readily open along the inner (upper) suture after fall or winter rains wet them, long after the plant has died" (p. 29).

Diplacus pygmaeus was segregated by Pennell as *Mimulus* sect. *Microphyton* on the basis of its highly reduced habit and the anthers of one pair smaller or lacking.

5. DIPLACUS sect. DIPLACUS

Perennial herbs from a woody caudex, subshrubs, or shrubs; leaf axils of main shoots often bearing tufts of narrower leaves; leaves often with revolute margins, commonly with a glutinous exudate; pedicels shorter than calyces; calyces prismatic 20–40 mm long; corolla persistent, 30–65 mm long; capsules linear-oblong, investing; styles glandular pubescent. x = 9.

(FNANM)

1. **Diplacus aridus** Abrams, Bull. Torrey Bot. Club 32: 540. 1905. *Mimulus aridus* (Abrams) A.L. Grant, Ann. Missouri Bot. Gard. 11: 336. 1925 ("1924").
2. **Diplacus aurantiacus** (Curtis) Jeps., Man. Fl. Pl. Calif. 919. 1925. *Mimulus aurantiacus* Curtis, Bot. Mag. 10: plate 354. 1796, non *M. aurantiacus* Renjifo 1884; *Diplacus glutinosus* var. *aurantiacus* (Curtis) Lindl., Paxt. Fl. Gard. 3: pl. 92. 1851.
   Diplacus glutinosus (J.C.Wendl.) Nutt., Ann. Nat. Hist. 1: 138. 1838. *Mimulus glutinosus* J.C.Wendl., Bot. Beob., 51. 1798.
3. **Diplacus x australis** (McMinn ex Munz) Tulig, Phytoneuron 2012-45: 16. 2012. *Diplacus australis* McMinn, Madroño 11: 58, 60, plate 12. 1951 (as species), nom. illeg. (without Latin diagnosis). *Mimulus aurantiacus* subsp. *australis* McMinn ex Munz, Aliso 4: 98. 1958. *Diplacus aurantiacus* subsp. *australis* (McMinn ex Munz) Beeks ex Thorne, Aliso 9: 194. 1978. [= *Diplacus longiflorus* x *D. puniceus*?]
4. **Diplacus calycinus** Eastw., Bot. Gaz. 41: 287. 1906. *Mimulus longiflorus* var. *calycinus* (Eastw.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 331. 1925 ("1924"). *Diplacus longiflorus* var. *calycinus* (Eastw.) Jeps., Man. Fl. Pl. Calif., 919. 1925. *Mimulus longiflorus* subsp. *calycinus* (Eastw.) Munz, Aliso 4: 99. 1958.
5. **Diplacus clevelandii** (Brandegee) Greene, Erythea 4: 22. 1896. *Mimulus clevelandii* Brandegee, Gard. & Forest 8: 134, plate 20. 1895.
6. **Diplacus grandiflorus** Groenland, Rev. Hort. [Paris] ser. 4, 6: 402, fig. 136. 1857 (not *Diplacus grandiflorus* Greene, 1890). *Diplacus longiflorus* var. *grandiflorus* (Groenland) Jepson, Man. Fl. Pl. Calif. 919. 1925. *Mimulus bifidus* Pennell, Proc Acad. Nat. Sci. Philadelphia 99: 168. 1947, nom. nov. (based on *D. grandiflorus* Groenland, blocked in *Mimulus* by *M. grandiflorus* Howell 1901 = *Erythranthe guttata*).
   Diplacus glutinosus var. *grandiflorus* Lindl. & Paxton, Paxt. Fl. Gard. 3: 96, plate 92. 1852. *Mimulus aurantiacus* var. *grandiflorus* (Lindl. & Paxton) D.M. Thompson, Monogr. Syst. Bot. 75: 158. 2005.
   Diplacus grandiflorus Greene, Pittonia 2: 156. 1890, nom. illeg. (not *Diplacus grandiflorus* Groenland 1857).
7. **Diplacus x linearis** (Benth.) Greene, Pittonia 2: 156. 1890 (as species). *Mimulus linearis* Benth., Scroph. Ind., 27. 1835. *Mimulus glutinosus* var. *linearis* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. *Mimulus longiflorus* var. *linearis* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 334. 1925 ["1924"]. *Diplacus longiflorus* var. *linearis* (Benth.) McMinn, Man. Calif, shrubs (ed. 1) 498. 1939. [= *Diplacus aurantiacus* x *D. calycinus*?]
   Mimulus bifidus subsp. *fasciculatus* Pennell, Proc. Acad. Nat. Ser. Philadelphia 99: 168. 1947. *Diplacus fasciculatus* (Pennell) McMinn, Madroño 11: 70. 1951.
8. **Diplacus x lompocensis** McMinn, Madroño 11: 62. 1951 (as species). *Mimulus aurantiacus* subsp. *lompocensis* (McMinn) Munz, Aliso 4: 99. 1958. [= *Diplacus aurantiacus* x *D. longiflorus*]

9. **Diplacus longiflorus** Nuttall, Ann. Nat. Hist. 1: 139. 1838. *Mimulus longiflorus* (Nutt.) A.L. Grant, Gentes Herb. 1: 136. 1923.
   Mimulus longiflorus var. *rutilus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 333. 1925 ("1924"). *Diplacus longiflorus* var. *rutilus* (A.L. Grant) McMinn, Man. Calif. Shrubs, 498. 1939. *Diplacus rutilus* (A.L. Grant) McMinn, Madroño 11: 83. 1951.
10. **Diplacus parviflorus** Greene, Pittonia 1: 36. 1887. *Mimulus parviflorus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 344. 1925 ("1924") (not *Mimulus parviflorus* Lindley 1825). *Mimulus flemingii* Munz, nom. nov., Man. S. Calif. Bot., 477, 601. 1935. *Mimulus aurantiacus* var. *parviflorus* (Greene) D.M.Thomps., Syst. Bot. Monogr. 75: 157. 2005.
11. **Diplacus puniceus** Nutt., Ann. Nat. Hist. 1: 137. 1838. *Mimulus puniceus* (Nutt.) Steud., Nomencl. Bot. (ed. 2) 2: 150. 1841. *Diplacus glutinosus* var. *puniceus* (Nutt.) Benth. in DC., Prodr. 10: 368. 1846. *Mimulus glutinosus* var. *puniceus* (Nutt.) A. Gray, Bot. California 1: 566. 1876. *Mimulus aurantiacus* var. *puniceus* (Nutt.) D.M.Thomps., Syst. Bot. Monogr. 75: 156. 2005.
12. **Diplacus rutilus** (A.L. Grant) McMinn, Madroño 11: 83. 1951. *Mimulus longiflorus* var. *rutilus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 333. 1925 ("1924"). *Diplacus longiflorus* var. *rutilus* (A.L. Grant) McMinn, Man. Calif. Shrubs, 498. 1939.

(MEXICO)

13. **Diplacus stellatus** Kellogg, Proc. Calif. Acad. Sci. 2: 18. 1863. *Diplacus glutinosus* var. *stellatus* (Kellogg) Greene, Pittonia 2: 155. 1890. *Mimulus stellatus* (Kellogg) A.L. Grant, Ann. Missouri Bot. Gard. 11: 337. 1925 ("1924").

Taxonomy of sect. *Diplacus* is discussed in detail by McMinn (1951), Beeks (1962), Waayers (1996), Tulig (2000), Thompson (2005), and most recently by Tulig and Nesom (2012). The taxa indicated to be hybrid in origin appear to behave essentially as species.

6. **DIPLACUS** sect. **CLEISANTHUS** (J.T. Howell) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* sect. *Cleisanthus* J.T. Howell, Leafl. W. Bot. 2: 80. 1938. **TYPE**: *Mimulus cleistogamus* J.T. Howell [= *Diplacus douglasii*]. The original circumscription of the section included only *M. cleistogamus*.

Annual, puberulent-glandular to pilose-glandular; flowers 2 per node; pedicels shorter than calyces; corollas purple to violet, bilabiate to subbilabiate or nearly radial, broadly funnelform-rotate, tube-throats narrowly cylindric, much longer than the calyx to barely longer, persistent; anthers hairy; styles glandular-pubescent; stigmas unequal, the lower longer; capsules indurate, often basally asymmetric, indehiscent. x = 9.

(FNANM)

1. **Diplacus congdonii** (B.L. Rob.) G.L. Nesom, **comb. nov.** *Mimulus congdonii* B.L. Rob., Proc. Amer. Acad. Arts 26: 175. 1891. *Eunanus congdonii* (B.L. Rob.) Greene, Erythea 1: 247. 1893.
2. **Diplacus douglasii** (Benth.) G.L. Nesom, **comb. nov.** *Eunanus douglasii* Benth. in DC., Prodr. 10: 374. 1846. *Mimulus douglasii* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876.
   Mimulus cleistogamus J.T.Howell, Leafl. West. Bot. 2: 79. 1938.
3. **Diplacus kelloggii** (Curran ex Greene) G.L. Nesom, **comb. nov.** *Eunanus kelloggii* Curran ex Greene, Bull. Calif. Acad. Sci. 1: 100. 1885. *Mimulus kelloggii* (Curran ex Greene) Curran ex A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1, Suppl.): 443. 1886.
4. **Diplacus latifolius** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus latifolius* A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876.
5. **Diplacus torreyi** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus torreyi* A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876. *Eunanus torreyi* (A. Gray) Greene, Bull. Calif. Acad. Sci. 1: 104. 1885.
6. **Diplacus traskiae** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus traskiae* A.L. Grant, Field Mus. Nat. Hist., Bot. Ser. 5: 226. 1923.

Sect. *Cleisanthus* is supported (bootstrap value = 84) in the molecular analysis of Beardsley et al. (2004) as sister to sect. *Diplacus*. Thompson (2005) placed *Diplacus torreyi* in *Mimulus* sect. *Eunanus* apparently because of its promptly dehiscent capsules with fragile walls (vs. tardily dehiscent with indurate walls), but molecular data indicate that it is sister to species 1–5 (above) of sect. *Cleisanthus*. *Diplacus torreyi* also differs from the other five species in chromosome number ($2n$ = 20 in *D. torreyi* vs. $2n$ = 18 in the others). In their combination of 2-flowered nodes and unequal stigma lobes, however, the six species of sect. *Cleisanthus* are morphologically coherent.

Thompson (2005, p. 29) noted that this group of species (he did not include *Mimulus torreyi* in his discussion) is characterized by unequal stigma lobes, ovate to rounded cotyledons, epigeous hypocotyls, two flowers per node, and their variety of habitats but never including vernally wet depressions or seepages. Also as observed by Thompson, the pedicel often twists 180° after anthesis in *D. congdonii* and *D. kelloggii*, inverting the developing fruit.

XII. LEUCOCARPUS D. Don in Sweet, Brit. Flower Gard. ser. 2, 2: pl. 124. 1831. *Mimulus* sect. *Leucocarpus* (D. Don) G.L. Nesom, Phytoneuron 2011-36: 4. 2011. **TYPE**: *Leucocarpus alatus* (Graham) Benth. [= *Leucocarpus perfoliatus*]

Plants shrubs or suffrutescent perennial herbs, **Vestiture**: glabrous or subglabrous, eglandular. **Stems** lignescent, strongly 4-angled to shallowly winged, erect. **Leaves** sessile (auriculate-clasping and perfoliate), thickened, not glandular-punctate, venation eucamptodromous. **Flowers** in axillary, pedunculate cymes of (1–)2–7(–14), on short, bracteate pedicels. **Fruiting pedicels** shorter to about equal to slightly longer than the calyces. **Fruiting calyces** erect, tube midveins strongly rounded-winged in the distal 2/3. **Corollas** yellow or white with a yellow throat, deciduous, limbs bilabiate. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** axile; **stigmas** bilamellate. **Fruits** white berries with thin skin and with most of the substance derived from the fleshy placenta, glabrous, septicidally sulcate, indehiscent. **Seed** surface reticulate. **Chromosome number** unknown. **Species** 1.

(MEXICO, CENTRAL AMERICA, SOUTH AMERICA)

1. Leucocarpus perfoliatus (Kunth) Benth. in DC., Prodr. 10: 335. 1846. *Mimulus perfoliatus* Kunth, Nov. Gen. Sp. (quarto ed.) 2: 371. 1817 [1818].

Conobea alata J. Graham, Edinburgh New Philos. J. 10: 168. 1830. *Leucocarpus alatus* (J. Graham) Benth., Brit. Flower Gard. ser. 2, 2: pl. 124. 1833[1831].

Leucocarpus perfoliatus ranges from Mexico (Chiapas, Guerrero, Hidalgo, Jalisco, [Michoacan?], Oaxaca, Puebla, Querétaro, San Luis Potosí, Veracruz) and Central America (Panama, Nicaragua, Honduras, Guatemala) southward to South America (Bolivia, Colombia, Ecuador, Peru, Venezuela). It occurs at elevations of 450–3100 meters. The distinct habit (erect, up to 2.5 m tall), large and thickened-succulent leaves, pedunculate cymes, large flowers, baccate fruits, and subtropical distribution of *Leucocarpus perfoliatus* are specialized within American Phrymaceae.

XIII. ERYTHRANTHE Spach, Hist. Nat. Veg. Phan. 9: 312. 1838 ["1840"]. *Mimulus* § *Erythranthe* (Spach) Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. **TYPE**: *Erythranthe cardinalis* (Douglas ex Benth.) Spach, the only species in the protologue.

Annual (fibrous-rooted or taprooted) or **perennial** (rhizomatous), terrestrial or semi-aquatic. **Vestiture**: glabrous, puberulent-glandular or villous-glandular, or hirtellous to hirsute, or a combination. **Stems** herbaceous, prostrate to decumbent or erect, terete or 4-angled. **Leaves** petiolate or sessile, herbaceous, often glandular-punctate, venation basal to suprabasal acrodromous. **Flowers** apparently solitary or axillary in bracteate, corymboid or racemose groupings. **Fruiting**

pedicels usually distinctly longer than calyces. **Fruiting calyces** erect or nodding, tube midveins weakly to strongly angled or wing-angled. **Corollas** deciduous (marcescent only in *E. breweri* and a few species of sect. *Simiola*), limbs strongly to weakly bilabiate or nearly regular. **Stamens** 4, anthers 2-celled. **Ovaries** 2-locular; **placentation** axile; **stigmas** bilamellate. **Fruits** many-seeded capsules and blunt or rounded to slighty emarginate apices, glabrous, loosely enclosed in persistent calyx, included, bilocular, loculicidally dehiscent to base along outer suture or both sutures, placentae fused in the basal half or for the whole length, remaining fused in fruit dehiscence. **Seed** surface reticulate to nearly smooth. **Chromosome numbers** $2n$ = 26, 28, 30, 32, 48, 56, 60, 62, 64, 92 (x = 14, 15). **Species** 111.

In adapting to the new generic name, audial memories will need to adjust in some cases to feminine forms of epithets (versus masculine in *Mimulus*). *Mimetanthe* Greene is similar, as is *Eremanthe* Spach (Clusiaceae).

Three revisionary treatments of *Erythranthe* sections, published simultaneous with this conspectus, provide full and detailed synonymy for complex groups (Nesom 2012b, 2012a, 2012c).

1. **ERYTHRANTHE** sect. **ACHLYOPITHECA** N.S. Fraga & G.L. Nesom, **sect. nov.** **TYPE**: *Erythranthe inconspicua* (A. Gray) G.L. Nesom & N.S. Fraga

Annual, usually glabrous; basal leaves in rosette or absent, cauline sessile, blades broadly elliptic to ovate or broadly ovate; fruiting pedicels usually longer than calyces; calyx swollen in fruit; corollas usually rose to light lavender, less commonly yellowish, caducous, limbs weakly bilabiate, lobes oblong-obovate to oblong with prominently notched apices, ventral ridges yellow-lined; anthers pubescent. x unknown.

(FNANM)

1. **Erythranthe inconspicua** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus inconspicuus* A. Gray, Pacif. Railr. Rep. 4: 120. 1857.
2. **Erythranthe acutidens** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus acutidens* Greene, Bull. Calif. Acad. Sci. 1: 117. 1885. *Mimulus inconspicuus* var. *acutidens* (Greene) A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 450. 1886.
3. **Erythranthe grayi** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus grayi* A.L. Grant, Ann. Missouri Bot. Gard. 11: 203. 1925 ("1924").

Mimulus acutidens and *M. grayi* have recently been included as synonyms of *M. inconspicuus* (e.g. Thompson 1993) but the three species are distinct and non-intergrading (Nesom 2012c).

2. **ERYTHRANTHE** sect. **PARADANTHA** (A.L. Grant) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* sect. *Paradanthus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"). **LECTOTYPE** (designated here): *Mimulus rubellus* A. Gray [= *Erythranthe rubella*]. Grant specified only that sect. *Paradanthus* comprised "Sp. 26–69" but observed that "*M. rubellus* is at the center of the section" and is closely allied with members of the *Mimulus palmeri* group.

Annual, stems and leaves glabrous, sessile to subsessile, sometimes clasping and fused; leaf blades linear-oblong to narrowly oblong-lanceolate or narrowly oblanceolate, entire or sometimes toothed, palmately 3-veined or sometimes pinnately veined (*E. barbata, E. montioides*); fruiting pedicels longer than calyces; calyces with sharp, definite angles and flat sides (except *E. montioides* and *E. discolor*); corollas pink to purplish, yellow, white, or bicolored, throats and ventral ridges

contrasting or same color, deciduous, limbs strongly to weakly bilabiate or nearly radial, lobes deeply to shallowly notched to entire. x = 8.

(FNANM)

1. **Erythranthe androsacea** (Curran ex Greene) N.S. Fraga, **comb. nov.** *Mimulus androsaceus* Curran ex Greene, Bull. Calif. Acad. Sci. 1: 121. 1885. *Mimulus palmeri* var. *androsaceus* (Curran ex Greene) A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 451. 1886.
2. **Erythranthe barbata** (Greene) N.S. Fraga, **comb. nov.** *Mimulus barbatus* Greene, Bull. Calif. Acad. Sci. 1: 9. 1884.
3. **Erythranthe diffusa** (A.L. Grant) N.S. Fraga, **comb. nov.** *Mimulus diffusus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 254. 1925 ("1924").
4. **Erythranthe discolor** (A.L. Grant) N.S. Fraga, **comb. nov.** *Mimulus discolor* A.L. Grant, Ann. Missouri Bot. Gard. 11: 257. 1925 ("1924").
5. **Erythranthe gracilipes** (B.L. Rob.) N.S. Fraga, **comb. nov.** *Mimulus gracilipes* B.L.Rob., Proc. Amer. Acad. Arts 26: 176. 1891.
6. **Erythranthe montioides** (A. Gray) N.S. Fraga, **comb. nov.** *Mimulus montioides* A. Gray, Proc. Amer. Acad. Arts 7: 380. 1868.
7. **Erythranthe palmeri** (A. Gray) N.S. Fraga, **comb. nov.** *Mimulus palmeri* A. Gray, Proc. Amer. Acad. Arts 12: 82. 1876.
8. **Erythranthe purpurea** (A.L. Grant) N.S. Fraga, **comb. nov.** *Mimulus purpureus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 255. 1925 ("1924").
9. **Erythranthe rubella** (A. Gray) N.S. Fraga, **comb. nov.** *Mimulus rubellus* A. Gray, Rep. U.S. Mex. Bound. 2(1): 116. 1859.
10. **Erythranthe shevockii** (Heckard & Bacig.) N.S. Fraga, **comb. nov.** *Mimulus shevockii* Heckard & Bacig., Madroño 32: 271. 1986.
11. **Erythranthe suksdorfii** (A. Gray) N.S. Fraga, **comb. nov.** *Mimulus suksdorfii* A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1, Suppl.): 450. 1886.

Erythranthe rubella is placed in sect. *Monimanthe* in the molecular phylogeny by Beardsley et al. (2004), but four samples of the species — a yellow form and a pink form, geographically separated — in a preliminary analysis by Fraga (in prep.) place it among the species of sect. *Paradantha*, closely related to *E. suksdorfii*. At least five species of sect. *Paradantha* remain to be described (Fraga 2011 and in prep.). The single author of the combinations is deliberate.

3. ERYTHRANTHE sect. **MONANTHA** G.L. Nesom & N.S. Fraga, **sect. nov.** **TYPE**: *Erythranthe primuloides* (Benth.) G.L. Nesom & N.S. Fraga

Perennial, rhizomatous, glabrous; leaves all basal or near-basal on stems with short internodes, sessile, blades oblanceolate-oblong, palmately veined, fleshy-coriaceous; fruiting pedicels erect, much longer than calyces, 1-flowered; corollas yellow, limbs weakly to strongly bilabiate, each of the three ventral lobes usually red-spotted. x = 9.

(FNANM)

1. **Erythranthe linearifolia** (A.L. Grant) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus primuloides* var. *linearifolius* A.L. Grant, Ann. Missouri Bot. Gard. 11: 246. 1925 ("1924"). *Mimulus linearifolius* (A.L. Grant) Pennell, Ill. Fl. Pacific States 3: 698. 1951. *Mimulus primuloides* subsp. *linearifolius* (A.L. Grant) Munz, Aliso 4: 99. 1958.
2. **Erythranthe primuloides** (Benth.) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus primuloides* Benth., Scroph. Ind., 29. 1835.

   Mimulus pilosellus Greene, Erythea 4: 22. 1896. *Mimulus primuloides* var. *pilosellus* (Greene) Smiley, Univ. Calif. Publ. Bot. 9: 332. 1921.

   Mimulus nevadensis Gand., Bull. Soc. Bot. France 19: 218. 1919.

4. ERYTHRANTHE sect. **MONIMANTHE** (Pennell) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* sect. *Monimanthe* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 167. 1947. **TYPE**: *Mimulus breweri* (Greene) Coville [= *Erythranthe breweri*]

Annual; stems and leaves glandular-puberulent; leaves sessile to subsessile, blades oblanceolate to narrowly oblanceolate; fruiting pedicels as long or longer than calyces; calyx eciliate at apex, ribs corky (a distinctive feature of this group), teeth 1–2 mm long; corollas violet to purple with darker throat and yellow ventral ridges (*M. breweri* and *M. filicaulis*) or yellow and white (*M. bicolor*), limbs strongly to weakly bilabiate (*M. bicolor*, *M. breweri*) to nearly radially symmetric (*M. filicaulis*); anthers hairy. x = 8.

(FNANM)

1. **Erythranthe bicolor** (Hartweg ex Benth.) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus bicolor* Hartweg ex Benth., Pl. Hartw. 328. 1849.
2. **Erythranthe breweri** (Greene) G.L. Nesom & N.S. Fraga, **comb. nov.** *Eunanus breweri* Greene, Bull. Calif. Acad. Sci. 1: 101. 1885. *Mimulus breweri* (Greene) Coville, Contr. U.S. Natl. Herb. 4: 171. 1893. *Mimulus rubellus* var. *breweri* (Greene) Jeps., Man. Fl. Pl. Calif., 927. 1925.
3. **Erythranthe filicaulis** (S. Watson) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus filicaulis* S. Watson, Proc. Amer. Acad. Arts 26: 125. 1891.
   Mimulus biolettii Eastw., Proc. Calif. Acad. Sci., ser. 3, 2: 290. 1902.

In the original description of sect. *Monimanthe*, which included only the type, *Mimulus breweri*, Pennell (1947, pp. 167-168) noted that it was "midway between the subgenera *Synplacus* and *Schizoplacus* of Grant; as already explained, it has the unsplit septum of the capsule of the former, but the corollas are only tardily deciduous [marcescent] as in the latter." Molecular data show the gynoecial character to be of stronger predictive value, and the relatively long pedicels also are indicative of its placement among the species of *Erythranthe*.

5. ERYTHRANTHE sect. **ERYTHRANTHE**

Perennial or (in *E. parishii*) annual, stems and leaves glabrous to puberulent or hirsute, sometimes glandular; leaf blades oblanceolate to narrowly lanceolate, shallowly toothed, palmately veined; fruiting pedicels longer than calyces; calyces with sharp, definite angles and flat sides; corollas deciduous, large (40–50 mm long), strongly red or magenta to pink, purplish, or (in *E. parishii*) nearly white, limbs bilabiate, lobes shallowly notched to slightly retuse or entire. x = 8.

(FNANM)

1. **Erythranthe cardinalis** (Douglas ex Benth.) Spach, Hist. Nat. Veg. 9: 313. 1840. *Mimulus cardinalis* Douglas ex Benth., Scroph. Ind. 28. 1835.
2. **Erythranthe eastwoodiae** (Rydb.) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus eastwoodiae* Rydb., Bull. Torrey Bot. Club 40: 483. 1913.
3. **Erythranthe lewisii** (Pursh) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus lewisii* Pursh, Fl. Amer. Sept. 2: 427. 1814.
   Mimulus lewisii var. *tetonensis* A. Nelson, Bot. Gaz. 34: 31. 1902. *Mimulus lewisii* forma *tetonensis* (A. Nelson) J.F. Macbr. & Payson, Contr. Gray Herb. 49: 67. 1917.

Various botanists have observed a difference in corolla color between the Sierra Nevada populations in California (mostly whitish to pink) of *Erythranthe lewisii* and those of the rest of the range (mostly purplish, including var. *tetonensis*). The type, from the "head springs of the Missouri," is described and illustrated by Pursh with a "beautiful pale purple" corolla. This pattern and an appropriate nomenclature remain to be worked out and documented.

4. **Erythranthe parishii** (Greene) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus parishii* Greene, Bull. Calif. Acad. Sci. 1: 108. 1885.

Greene (1885) placed *Erythranthe parishii* with *E. cardinalis* and *E. lewisii* (constituting *Mimulus* sect. *Erythranthe*) but the evolutionary position of this annual, white-flowered species among the otherwise perennial, red- and purple-flowered species was first unequivocally demonstrated by Beardsley et al. (2003, 2004).

5. **Erythranthe verbenacea** (Greene) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus verbenaceus* Greene, Leafl. Bot. Observ. Crit. 2: 2. 1909. *Mimulus cardinalis* var. *verbenaceus* (Greene) Kearney & Peebles, J. Wash. Acad. Sci. 29: 491. 1939.

(NORTH AMERICA-Mexico)

6. **Erythranthe nelsonii** (A.L. Grant) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus nelsonii* A.L. Grant, Ann. Missouri Bot. Gard. 11: 144. 1925 ("1924").
7. **Erythranthe rupestris** (Greene) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus rupestris* Greene, Leafl. Bot. Obs. Crit. 2: 3. 1909.

6. **ERYTHRANTHE** sect. **ALSINIMIMULUS** G.L. Nesom & N.S. Fraga, **sect. nov. TYPE**: *Erythranthe alsinoides* (Douglas ex Benth.) G.L. Nesom & N.S. Fraga

Annual, villous-hirsute to puberulent, often glandular; leaf blades palmately veined, broadly ovate to subrotund, margins shallowly serrate-dentate to denticulate; fruiting pedicels longer than calyces; calyx margins nearly truncate; corollas tiny, yellow, palate usually with a single, large red-purple spot, each of the upper lobes medially purple-striped, limbs strongly bilabiate, throats open; stamens exserted. x unknown.

(FNANM)

1. **Erythranthe alsinoides** (Douglas ex Benth.) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus alsinoides* Douglas ex Benth., Scroph. Ind., 29. 1835.
   Mimulus alsinoides var. *minimus* Benth., Scroph. Ind., 29. 1835.

Erythranthe alsinoides, according to the molecular analysis, has a sister relationship to the clade comprising sect. *Sinopitheca* and sect. *Mimulasia*, but this relationship has weak support and *E. alsinoides* is very different in morphology. Gray (1886, p. 449) described the calyx as "campanulate-oblong, hardly at all unequal-sided at maturity or ventricose, but nearly filled by the oblong capsule; the short-toothed orifice as if truncate and moderately oblique." Grant (1924, p. 234) noted that "*M. alsinoides* is most closely related to *M. pulsiferae* [placed here in sect. *Mimulosma*] with which it has often been confused. The unequal calyx-teeth, 2 of which are truncate and longer than the 3 triangular-acute upper ones, distinguish this species from any other *Mimulus* except *M. pachystylus* [here identified as *Erythranthe orizabae*, sect. *Mimulasia*]."

7. **ERYTHRANTHE** sect. **SIMIGEMMA** G.L. Nesom & N.S. Fraga, **sect. nov. TYPE**: *Erythranthe gemmipara* (W.A. Weber) G.L. Nesom & N.S. Fraga

Annual; glabrous; petioles laterally compressed and deeply saccate at the base, usually containing a lenticular propagule; fruiting pedicels slightly longer than calyces; calyx strongly angled, weakly inflated; corollas yellow, not spotted or striped, limbs weakly bilabiate, throats open. x = 8.

(FNANM)

1. **Erythranthe gemmipara** (W.A. Weber) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus gemmiparus* W.A. Weber, Madroño 21: 423. 1972.

Production of bulbils enclosed within a saccate petiole is unique within the genus (Moody et al. 1999). Flowers are uncommon. Seed production has been documented in the greenhouse, but seed formation has not been documented in nature. *Erythranthe gemmipara* is known only from eight populations in north-central Colorado.

8. ERYTHRANTHE sect. **MIMULOSMA** G.L. Nesom & N.S. Fraga, **sect. nov. TYPE**: *Erythranthe moschata* (Douglas ex Lindl.) G.L. Nesom & N.S. Fraga

Annual or perennial; vestiture of viscid or gland-tipped hairs, sometimes aromatic; leaves palmately or subpinnately veined (weakly suprabasal-acrodromous); fruiting pedicels longer than calyces; calyx teeth usually small and usually of equal or subequal length; corollas yellow, rarely white, commonly red-spotted in the throat, limbs strongly to weakly bilabiate or nearly regular. x = 8.

(FNANM)

1. **Erythranthe ampliata** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus ampliatus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 214. 1925 ("1924").
2. **Erythranthe arenaria** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus arenarius* A.L. Grant, Ann. Missouri Bot. Gard. 11: 215. 1925 ("1924").
   Mimulus multiflorus Pennell, Proc. Acad. Nat. Sci. Philad. 99: 161. 1947.
   Mimulus trisulcatus Pennell, Proc. Acad. Nat. Sci. Philad. 99: 161. 1947.
   Mimulus floribundus var. *subulatus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 222. 1925 ("1924").
3. **Erythranthe breviflora** (Piper) G.L. Nesom, **comb. nov.** *Mimulus breviflorus* Piper, Bull. Torrey Bot. Club 28: 45. 1901.
4. **Erythranthe floribunda** (Douglas ex Lindl.) G.L. Nesom, **comb. nov.** *Mimulus floribundus* Douglas ex Lindl., Bot. Reg. 13: pl. 1125. 1828.
   Mimulus pubescens Benth. in DC., Prodr. 10: 372. 1846. Placed here tentatively in synonymy but perhaps to be recognized as a good species — see Nesom (2012b).
5. **Erythranthe geniculata** (Greene) G.L. Nesom, **comb. nov.** *Mimulus geniculatus* Greene, Bull. Calif. Acad. Sci. 1: 280. 1885.
   Mimulus dudleyi A.L. Grant, Ann. Missouri Bot. Gard. 11: 235. 1925 ("1924").
6. **Erythranthe hymenophylla** (Meinke) G.L. Nesom, **comb. nov.** *Mimulus hymenophyllus* Meinke, Madroño 30: 147. 1983.
7. **Erythranthe inflatula** (Suksd.) G.L. Nesom, **comb. nov.** *Mimulus inflatulus* Suksd., Werdenda 1: 38. 1927.
   Mimulus evanescens Meinke, Great Basin Naturalist 55: 250. 1995.
8. **Erythranthe inodora** (Greene) G.L. Nesom, **comb. nov.** *Mimulus inodorus* Greene, Bull. Calif. Acad. Sci. 1: 119. 1885.
   Mimulus moschatus var. *sessilifolius* A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 447. 1886.
9. **Erythranthe jungermannioides** (Suksd.) G.L. Nesom, **comb. nov.** *Mimulus jungermannioides* Suksd., Deutsche Bot. Monatsschr. 18: 154. 1900.
10. **Erythranthe latidens** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus inconspicuus* A. Gray var. *latidens* A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1, Suppl.): 450. 1886. *Mimulus latidens* (A. Gray) Greene, Man. Bot. San Francisco, 278. 1894.
11. **Erythranthe moniliformis** (Greene) G.L. Nesom, **comb. nov.** *Mimulus moniliformis* Greene, Bull. Calif. Acad. Sci. 1: 10. 1884. *Mimulus moschatus* var. *moniliformis* (Greene) Munz, Aliso 4: 99. 1958.
    Mimulus dentatus var. *gracilis* A. Gray, Bot. Gaz. 7: 112. 1882.
    Mimulus leibergii A.L. Grant, Ann. Missouri Bot. Gard. 11: 231, pl. 6, f. 1. 1925 ("1924").
    Mimulus macranthus Pennell, Proc. Acad. Philad. 99: 160. 1947.
    Mimulus moschatus var. *longiflorus* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 2: 278. 1886; 2(1): 447. 1886.
12. **Erythranthe moschata** (Douglas ex Lindl.) G.L. Nesom, **comb. nov.** *Mimulus moschatus* Douglas ex Lindl., Bot. Reg. 13: plate 1118. 1828.
    Mimulus crinitus A.L. Grant, Ann. Missouri Bot. Gard. 11: 186. 1925 ("1924"). *Mimulus acutidens* Reiche, Fl. Chile 6: 63. 1911 (non *M. acutidens* Greene 1885.

13. **Erythranthe norrisii** (Heckard & Shevock) G.L. Nesom, **comb. nov.** *Mimulus norrisii* Heckard & Shevock, Madroño 32: 179. 1985.
14. **Erythranthe patula** (Pennell) G.L. Nesom, **comb. nov.** *Mimulus patulus* Pennell, Proc. Acad. Nat.l Sci. Philadelphia 99: 162. 1947.
15. **Erythranthe pulsiferae** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus pulsiferae* A. Gray, Proc. Amer. Acad. Arts 11: 98. 1876.
16. **Erythranthe washingtoniensis** (Gand.) G.L. Nesom, **comb. nov.** *Mimulus washingtoniensis* Gand., Bull. Soc. Bot. France 66: 218. 1919.

(NORTH AMERICA -Mexico)
17. **Erythranthe austrolatidens** G.L. Nesom, Phytoneuron 2012-41: 23. 2012.

(ASIA-southeastern Russia)
18. **Erythranthe stolonifera** (Novopokr.) G.L. Nesom, **comb. nov.** *Mimulus stolonifer* Novopokr., Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 11: 158. 1949.

Pennell (1935) noted that the Chilean *Mimulus acutidens* Reiche of 1911 (not Greene 1885) is the same species as the North American *M. moschatus*. Von Bohlen (1995b) maintained the Chilean entity as a distinct species — *M. crinitus* (incl. *M. acutidens* Reiche as a synonym) — but noted that a closer analysis of North American material of *M. moschatus* is necessary for a better judgement. Present studies (Nesom 2011b) corroborate Pennell's assessment. Von Bohlen also placed the Chilean *Mimulus bridgesii* in this relationship (sect. *Mimulosma*), especially based on similarities in calyx and pollen morphology, but that species is placed here in the otherwise Asian *Erythranthe* sect. *Sinopitheca*.

Sect. *Mimulosma* (as considered here) has been studied recently by Argue (1986) and Whittall et al. (2006). *Erythranthe latidens* is portrayed in the molecular analysis as phylogenetically basal to the whole section, and evidence suggests that *E. inflatula* is of hybrid origin between *E. latidens* and *E. breviflora*. *Erythranthe arenaria* was not included in the molecular samples of Whittall et al. — pollen and leaf morphology as well as geography place it in the Sierra Nevada clade. *Erythranthe macrantha* and *E. moniliformis* have recently been treated as conspecific with *E. moschata* but are considered here to be distinct taxa. The extra-North American species have not yet been included in a molecular study.

Two pollen types were recognized among species of the "*Mimulus moschatus* alliance" by Argue (1986). Most of the species, including *M. moschata*, have the *sexine 2* configuration, predominantly microreticulate with supramurial granules or spinules, known as *type IIc*: The pollen of *E. arenaria*, *E. geniculata*, *E. floribunda*, and *E. moniliformis* is *type IIb*, lacking supramurial granules or spinules. Argue noted that the segregation of *E. moniliformis* and *E. inodora* from *E. moschata* is supported by these observations.

A detailed study of sect. *Mimulosma* (Nesom 2012b), published simultaneously with the present manuscript, includes maps, typifications, synonymy, descriptions, and a key to the species.

9. **ERYTHRANTHE** sect. **MIMULASIA** G.L. Nesom & N.S. Fraga, **sect. nov.** **TYPE**: *Erythranthe tenella* (Bunge) G.L. Nesom & N.S. Fraga

Mimulus § *Teneri* Benth. in DC., Prodr. 10: 372. 1846. **LECTOTYPE** (designated here): *Mimulus tenellus* Bunge. In addition to *M. nepalensis*, *M. tenellus* and *M. dentatus*, Bentham also included *M. alsinoides*, *M. floribundus*, *M. pubescens*, *M. moschatus*, and *M. orizabae* in § *Teneri*. The last five species are placed here into three other sections, thus Bentham's group was polyphyletic. The choice of type must be from among *M. nepalensis*, *M. tenellus*, and *M.*

dentatus, and because the position of *M. dentatus* is not unequivocal, an Asian species is chosen.

Perennial, rhizomatous; glabrous to sparsely villous or villous-hirsute, eglandular (or in *E. karakormiana*) glandular; stems quadrangular, sometimes narrowly winged; leaves petiolate, blades ovate to ovate-triangular, ovate-oblong, or suborbicular, pinnately to subpinnately veined (strongly suprabasal-acrodromous), margins coarsely serrate; fruiting pedicels usually slightly longer than calyces; corollas yellow to golden yellow, sometimes red-spotted or with a purple patch, tube-throat barely or slightly exserted from the calyx (more so in *E. dentata*), limbs strongly bilabiate, throats open; style exserted. x = 8 (2*n* = 32 reported for *E. nepalensis* by Probatova and Sokolovskaya 1986).

(ASIA-Himalayas)

1. **Erythranthe bhutanica** (Yamazaki) G.L. Nesom, **comb. nov.** *Mimulus bhutanicus* Yamazaki, J. Jap. Bot. 68: 23. 1993.
2. **Erythranthe bodinieri** (Vaniot) G.L. Nesom, **comb. nov.** *Mimulus bodinieri* Vaniot, Bull. Acad. Int. Géogr. Bot. 15(185–186): 86. 1905.
3. **Erythranthe inflata** (Miq.) G.L. Nesom, **comb. nov**. *Torenia inflata* Miq., Ann. Mus. Bot. Lugd. Bat. 3: 192. 1867. *Mimulus inflatus* (Miq.) Nakai, Bot. Mag. (Tokyo) 33: 209. 1919.
   Mimulus nepalensis forma *japonicus* Miq., Prolusio Fl. Japon., 48. 1866. *Mimulus nepalensis* var. *japonicus* Miq., Mél Biol. 9: 401. 1874.
4. **Erythranthe karakormiana** (Yamazaki) G.L. Nesom, **comb. nov.** *Mimulus karakormianus* Yamazaki, J. Jap. Bot. 68: 26. 1993.
5. **Erythranthe nepalensis** (Benth.) G.L. Nesom, **comb. nov.** *Mimulus nepalensis* Benth., Scroph. Ind., 29. 1835. *Mimulus tenellus* var. *nepalensis* (Benth.) P.C.Tsoong ex H.P.Yang, Fl. Reipubl. Popularis Sin. 67(2): 171. 1979.
   Mimulus formosanus Hayata, Icon. Pl. Formosan. 9: 79. 1920.
   Mimulus assamicus Griff., Madras J. Lit. Sci. 4: 375. 1836.
6. **Erythranthe procera** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus nepalensis* Benth. var. *procerus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 207. 1925 ("1924"). *Mimulus tenellus* var. *procerus* (A.L. Grant) Hand.-Mazz., Symb. Sin. 7: 832. 1936.
7. **Erythranthe szechuanensis** (Y.Y. Pai) G.L. Nesom, **comb. nov.** *Mimulus szechuanensis* Y.Y. Pai, Contr. Inst. Bot. Natl. Acad. Peiping 2: 119. 1934.
8. **Erythranthe tenella** (Bunge) G.L. Nesom, **comb. nov.** *Mimulus tenellus* Bunge, Enum. Pl. China Bor., 49. 1833.
9. **Erythranthe sinoalba** G.L. Nesom, Phytoneuron 2012-44: 1. 2012.

Molecular data (Beardsley & Olmstead 2002; Beardsley et al. 2004) indicate that *Erythranthe bodinieri*, *E. nepalensis*, and *E. tenella* constitute a monophyletic group. *Mimulus tenellus* was treated by Hong et al. (1998) as having three varieties, *nepalensis*, *platyphyllus*, and *procerus*, in addition to var. *tenellus*. Differences between the taxa, however, are generally characteristic of those between different species, and based on the limited observations in the present study, intermediates do not occur. *Erythranthe szechuanensis*, *E. karakormiana*, and *E. bhutanensis* are similar to these in morphology and geography and are included in sect. *Mimulasia* on that basis. This whole group appears to be most closely related to the North American *Erythranthe* sect. *Mimulosma* (fide Beardsley et al. 2004). The Asian species are strongly erect and have sharply toothed leaves with acute apices; they also are distinct from sect. *Mimulosma* in vestiture but the characteristic glandularity of the American species is mirrored in *E. karakormiana* and to a lesser extent in *E. sinoalba*.

Mimulus platyphyllus and *M. tibeticus*, which have previously been allied with *Mimulus nepalensis*, have palmate (basal acrodromous) leaf venation and are placed here in *Erythranthe* sect. *Sinopitheca*.

(FNANM)

10. **Erythranthe dentata** (Nutt. ex Benth.) G.L. Nesom, **comb. nov.** *Mimulus dentatus* Nutt. ex Benth. in DC., Prodr. 10: 372. 1846.

Molecular data place *Erythranthe dentata* as sister to *E. sessilifolia* (sect. *Sinopitheca*) but the two species are different in leaf morphology. The sessile, palmately veined leaves of *E. sessilifolia* are a feature of two other Asian species (not included in the molecular analysis), which are placed here in its closer relationship. *Erythranthe dentata* may indeed prove to be most closely related to sect. *Sinopitheca* but the phylogeny needs to be re-examined in the context of additional species. At least, like *E. bridgesii* in South America and *E. orizabae* in Mexico and Central America, *E. dentata* appears to be phyletically isolated in its geographical area, with its closest relatives in Asia, either in sect. *Sinopitheca* or in sect. *Mimulasia*, plus one in Mexico and Central America (*E. orizabae*).

(NORTH AMERICA-Mexico and Central America)

11. **Erythranthe orizabae** (Benth.) G.L. Nesom, **comb. nov.** *Mimulus orizabae* Benth. in DC., Prodr. 10: 372. 1846.
Mimulus pachystylus A.L. Grant, Ann. Missouri Bot. Gard. 11: 234. 1925 ("1924").

Erythranthe orizabae is characterized by herbaceous, prostrate stems rooting at the nodes; young stems and adaxial leaf surfaces are arachnoid-villous with long, viscid, crinkly hairs sometimes with colored cross walls; leaf blades are ovate with serrate margins, bicolored with a lighter abaxial surface, and pinnately veined (strongly suprabasal-acrodromous). It is at least superficially similar to *E. moschata*, which usually has ascending-erect stems and concolorous leaves, but the vestiture of *E. orizabae* is only of relatively coarse eglandular hairs and in this respect (as well as leaf ventation) the species is more similar to sect. *Mimulasia*, which otherwise is strictly Asian. Collections of *E. orizabae* have been made from from Guatemala, Chiapas, Oaxaca, Hidalgo, and Veracruz (whence the type: K, photo MO!). See Nesom (2011d) for typification and other details.

10. ERYTHRANTHE sect. **SINOPITHECA** G.L. Nesom & N.S. Fraga, **sect. nov. TYPE**: *Erythranthe sessilifolia* (Maxim.) G.L. Nesom & N.S. Fraga

Perennial, rhizomatous; stems, pedicels, calyces, and leaves glabrous to subglabrous; leaves sessile, blades palmately veined, margins dentate; fruiting pedicels about equal to the subtending leaves or a little longer; calyces with shallowly lobed to subtruncate margins; corollas yellow, limbs bilabiate, broadly expanded with open throats. x unknown.

(ASIA-Himalayas and Japan)

1. **Erythranthe bracteosa** (P.C. Tsoong) G.L. Nesom, **comb. nov**. *Mimulus bracteosus* P.C. Tsoong, Acta Phytotax. Sin. 3: 415. 1955.
2. **Erythranthe platyphylla** (Franch.) G.L. Nesom, **comb. nov.** *Mimulus nepalensis* var. *platyphyllus* Franch., Nouv. Arch. Mus. Hist. Nat. 10: 103. 1888. *Mimulus tenellus* var. *platyphyllus* (Franch.) P.C.Tsoong ex H.P.Yang, Fl. Reipubl. Popularis Sin. 67: 171. 1979.
3. **Erythranthe sessilifolia** (Maxim.) G.L. Nesom, **comb. nov.** *Mimulus sessilifolius* Maxim., Bull. Acad. Petersb. 20: 436. 1874.
4. **Erythranthe tibetica** (P.C. Tsoong & H.P. Yang) G.L. Nesom, **comb. nov.** *Mimulus tibeticus* P.C. Tsoong & H.P. Yang, Fl. Reipubl. Popularis Sin. 67: 166, 399 (addenda), fig. 45. 1979.

Erythranthe bracteosa is differs from the other of these Himalayan species in its distinctly suprabasal-acrodromous venation (veins relatively few in number; Fig. 2) and linear calyx lobes, but it seems better placed here than in sect. *Mimulasia*. Venation in the Japanese *E. sessilifolia* also occasionally is weakly suprabasal.

(SOUTH AMERICA-Chile)

5. **Erythranthe bridgesii** (Benth.) G.L. Nesom, **comb. nov**. *Mimulus parviflorus* Lindl. var. *bridgesii* Benth. in DC., Prodr. 10: 371. 1846. *Mimulus bridgesii* (Benth.) Clos, Fl. Chil. [Gay] 5: 141. 1849. **TYPE**: **CHILE**. The protologue has this: "In Chili australi (Bridges! n. 686), in ins. Chiloe (Darwin!)." Holotype: K?

Erythranthe bridgesii is characterized by its apparently annual duration, decumbent-erect to ascending-erect stems rooting at proximal nodes, glabrous and eglandular herbage, sessile, ovate to lanceolate leaves, long fruiting pedicels (16–60 mm, often longest distally), calyces with barely differentiated lobes and subtruncate margins, and yellow, red-spotted corollas (throat, palate, and lobes) with tube-throats 6–8 mm and limbs distinctly expanded but weakly bilabiate, the lobes deeply notched. Von Bohlen (1995) placed the species in the relationship of *Mimulus moschatus* (as synonym *M. crinitus* A.L. Grant) and *M. floribundus* Douglas ex Lindl., especially based on similarities in pollen morphology (or its lack of similarity to sect. *Simiolus*), but its placement within sect. *Mimulosma* is problematic.

The nearly plicate calyx angles and the sessile, semisucculent, 3–5-palmately nerved leaves of *Erythranthe bridgesii* are similar to those of *Erythranthe* sect. *Simiolus*, which has radiated in Andean South America, but pollen morphology excludes it from that group (Argue 1981). The species is tentatively placed here as a continentally disjunct member of sect. *Sinopitheca*, with which it shares glabrous vestiture, sessile (cauline) and palmately veined leaves, calyces with shallowly lobed to subtruncate margins, and broadly spreading, weakly bilabiate to nearly regular limbs. Pollen of *E. bridgesii* is tetracolpate or pentacolpate in contrast to the tricolporate pollen of its putative Asian relatives, but this was viewed by Argue as a derived feature and does not negate the hypothesis of relationship offered here.

11. ERYTHRANTHE sect. **EXIGUA** G.L. Nesom & N.S. Fraga, **sect. nov. TYPE**: *Erythranthe exigua* (A. Gray) G.L. Nesom & N.S. Fraga

Annual; glandular-puberulent; leaf blades oblong-lanceolate; fruiting pedicels longer than calyces; calyces 2–3 mm long; corollas lavender, tube-throats 2–2.5 mm long, limbs bilabiate with an open throat; capsules mostly 3–3.5 mm long, longer than the calyces. x unknown.

(FNANM)

1. **Erythranthe exigua** (A. Gray) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus exiguus* A. Gray, Proc. Amer. Acad. Arts 20: 307. 1885.

Erythranthe exigua in the molecular analysis of Beardsley et al. (2004) is placed sister to sect. *Simiola* with poor support and is on a long branch. Plants of *Mimulus exiguus* are diminutive annuals with few nodes and greatly reduced leaves, corollas, and calyces. The corollas are lavender, the calyces do not have upcurving lower lips (as in sect. *Simiola*), and the mature capsules usually are distinctly exserted from the calyces.

12. ERYTHRANTHE sect. **SIMIOLA** (Greene) G.L. Nesom & N.S. Fraga, **comb. nov.** *Mimulus* § *Simiolus* Greene, Bull. Calif. Acad. Sci. 1: 109. 1885. **LECTOTYPE** (designated here): *Mimulus guttatus* Fisch. ex DC. [= *Erythranthe guttata*] *Mimulus guttatus* is chosen as the type because it often is considered the "central" species of the section, often regarded as inclusive of many of the other species or regarded as directly ancestral to them.

Mimulus § *Speciosi* Benth. in DC., Prodr. 10: 369. 1846. **LECTOTYPE** (designated here): *Mimulus luteus L. Mimulus luteus* is chosen here as lectotype because it is the "showiest" of the species listed by Bentham, corresponding to his epithet "speciosi."

Annual to short-lived perennial; hirtellous to hirsute or stipitate- to villous-glandular, sometimes a mixture; cauline leaf blades generally sessile and ovate (fused in *E. glaucescens*, dissected in *E. laciniata*), palmately veined; fruiting pedicels longer than calyces; fruiting calyx inflated and sagittally compressed with lower lobes characteristically turning up and folding over the lateral teeth, nearly closing the throat; corollas yellow (cream to pink or red in some Chilean species) commonly with with red spots along the throat, limbs strongly bilabiate, throat compressed and occluded by swollen ventral ridges of the lower lip. x = 8.

(FNANM)

1. **Erythranthe arenicola** (Pennell) G.L. Nesom, **comb. et stat. nov.** *Mimulus guttatus* subsp. *arenicola* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 166. 1947.
2. **Erythranthe arvensis** (Greene) G.L. Nesom, **comb. nov.** *Mimulus arvensis* Greene, Pittonia 1: 37. 1887. *Mimulus langsdorffii* var. *arvensis* (Greene) Jeps., Fl. W. Mid. Calif., 407. 1901. *Mimulus guttatus* var. *arvensis* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 174. 1925 ("1924"). *Mimulus guttatus* subsp. *arvensis* (Greene) Munz, Aliso 4: 99. 1958.
   Mimulus micranthus A. Heller, Muhlenbergia 8: 132. 1912. *Mimulus nasutus* Greene var. *micranthus* (A. Heller) A.L. Grant, Ann. Missouri Bot. Gard. 11: 331. 1925 ("1924"). *Mimulus guttatus* var. *micranthus* (A. Heller) G.R. Campbell, Aliso 2: 332. 1950. *Mimulus guttatus* subsp. *micranthus* (A. Heller) Munz, Aliso 4: 99. 1958.
3. **Erythranthe brachystylis** (Edwin) G.L. Nesom, **comb. nov.** *Mimulus brachystylis* Edwin, Leafl. W. Bot. 7: 137. 1954.
4. **Erythranthe brevinasuta** G.L. Nesom, Phytoneuron 2012-40: 70. 2012.
5. **Erythranthe caespitosa** (Greene) G.L. Nesom, **comb. nov.** *Mimulus scouleri* var. *caespitosus* Greene, Pittonia 2: 22. 1889. *Mimulus caespitosus* (Greene) Greene, J. Bot. (Brit. & Foreign) 33: 8. 1895. *Mimulus tilingii* var. *caespitosus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 154. 1925 ("1924").
6. **Erythranthe calciphila** (Gentry) G.L. Nesom, **comb. nov.** *Mimulus calciphilus* Gentry, Madroño 9: 2. 1947.
7. **Erythranthe charlestonensis** G.L. Nesom, Phytoneuron 2012-40: 80. 2012.
8. **Erythranthe chinatiensis** G.L. Nesom, Phytoneuron 2012-40: 86. 2012.
9. **Erythranthe cordata** (Greene) G.L. Nesom, **comb. nov.** *Mimulus cordatus* Greene, Leafl. Bot. Observ. Crit. 2: 6. 1909.
10. **Erythranthe decora** (A.L. Grant) G.L. Nesom, **comb. nov.** *Mimulus guttatus* var. *decorus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 173. 1925 ("1924"). *Mimulus decorus* (A.L. Grant) Suksd., Werdenda 1: 37. 1927.
11. **Erythranthe geyeri** (Torr.) G.L. Nesom, **comb. nov.** *Mimulus geyeri* Torr. in Nicollet, Rep. Hydrogr. Upper Mississippi, 157. 1843.
    Mimulus jamesii Torr. & A. Gray ex Benth. in DC., Prodr. 10: 371. 1846. *Mimulus p* var. *jamesii* (Torr. & A. Gray) A. Gray, Synopt. Fl. N. Amer. ed. 2, 2(1): Suppl. 447. 1886.
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12. **Erythranthe glaucescens** (Greene) G.L. Nesom, **comb. nov.** *Mimulus glaucescens* Greene, Bull. Calif. Acad. Sci. 1: 113. 1885. *Mimulus guttatus* var. *glaucescens* (Greene) Jeps., Man. Fl. Pl. Calif., 928. 1925.
13. **Erythranthe grandis** (Greene) G.L. Nesom, **comb. nov.** *Mimulus guttatus* var. *grandis* Greene, Man. Bot. San Francisco Bay, 277. 1894. *Mimulus grandis* (Greene) A.Heller, Muhlenbergia 1: 110. 1904. *Mimulus langsdorffii* var. *grandis* (Greene) Greene, J. Bot. (Brit. & Foreign) 33: 7: 1895. See South American taxa.
14. **Erythranthe guttata** (Fisch. ex DC.) G.L. Nesom, **comb. nov.** *Mimulus guttatus* Fisch. ex DC., Cat. Pl. Horti Monsp., 127. 1813. *Mimulus langsdorffii* var. *guttatus* (Fisch. ex DC.) Jeps., Fl. W. Mid. Calif., 406. 1901.
15. **Erythranthe hallii** (Greene) G.L. Nesom, **comb. nov.** *Mimulus hallii* Greene, Bull. Calif. Acad. Sci. 1: 113. 1885. *Mimulus guttatus* var. *hallii* (Greene) A.L. Grant. Ann. Missouri Bot. Gard. 11: 172. 1924.

16. **Erythranthe inamoena** (Greene) G.L. Nesom, **comb. nov.** *Mimulus inamoenus* Greene, Pittonia 5: 137. 1903.
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17. **Erythranthe laciniata** (A. Gray) G.L. Nesom, **comb. nov.** *Mimulus laciniatus* A. Gray, Proc. Amer. Acad. Arts 11: 98. 1876.
18. **Erythranthe marmorata** (Greene) G.L. Nesom, **comb. nov.** *Mimulus marmoratus* Greene, Erythea 3: 73. 1895.
    Mimulus whipplei A.L. Grant, Ann. Missouri Bot. Gard. 11: 184. 1925 ("1924").
19. **Erythranthe michiganensis** (Pennell) G.L. Nesom, **comb. nov.** *Mimulus glabratus* subsp. *michiganensis* Pennell, Acad. Nat. Sci. Philadelphia Monogr. 1: 119. 1935. *Mimulus glabratus* var. *michiganensis* (Pennell) Fassett, Rhodora 41: 524. 1939. *Mimulus michiganensis* (Pennell) Posto & Prather, Syst. Bot. 28: 177. 2003.
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21. **Erythranthe minor** (A. Nelson) G.L. Nesom, **comb. nov.** *Mimulus minor* A. Nelson, Proc. Biol. Soc. Wash. 17: 178. 1904.
22. **Erythranthe corallina** (Greene) G.L. Nesom, **comb. nov.** *Mimulus corallinus* Greene, Erythea 4: 21. 1896.
    Mimulus minusculus Greene, Leafl. Bot. Observ. Crit. 2: 5. 1909.
23. **Erythranthe nasuta** (Greene) G.L. Nesom, **comb. nov.** *Mimulus nasutus* Greene, Bull. Calif. Acad. Sci. 1: 112. 1885. *Mimulus langsdorffii* var. *nasutus* (Greene) Jeps., Fl. W. Calif., 407. 1901. *Mimulus guttatus* var. *nasutus* (Greene) Jeps., Man. Fl. Pl. Calif., 928. 1925.
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25. **Erythranthe pardalis** (Pennell) G.L. Nesom, **comb. nov.** *Mimulus pardalis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 164. 1947.
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26. **Erythranthe parvula** (Wooton & Standley) G.L. Nesom, **comb. nov.** *Mimulus parvulus* Wooton & Standley, Contr. U.S. Natl. Herb. 16: 171. 1913.
27. **Erythranthe regni** G.L. Nesom, Phytoneuron 2012-40: 24. 2012.
28. **Erythranthe scouleri** (Hook.) G.L. Nesom, **comb. nov.** *Mimulus scouleri* Hook., Fl. Bor.-Amer. 2: 100. 1838. *Mimulus guttatus* subsp. *scouleri* (Hook.) Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 166. 1947.
29. **Erythranthe thermalis** (A. Nelson) G.L. Nesom, **comb. nov.** *Mimulus thermalis* A. Nelson, Bull. Torrey Bot. Club 27: 269. 1900.
30. **Erythranthe tilingii** (Regel) G.L. Nesom, **comb. nov.** *Mimulus tilingii* Regel, Gartenflora 18: 321, plate 631. 1869. *Mimulus langsdorffii* var. *tilingii* (Regel) Greene, J. Bot. (Brit. & Foreign) 33: 8. 1895.
31. **Erythranthe unimaculata** (Pennell) G.L. Nesom, **comb. nov.** *Mimulus unimaculatus* Pennell, Notul. Nat. Acad. Nat. Sci. Philadelphia 43: 5. 1940.
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(NORTH AMERICA-Mexico)

33. **Erythranthe brevinasuta** G.L. Nesom, Phytoneuron 2012-40: 70. 2012.
34. **Erythranthe dentiloba** (B.L. Rob. & Fernald) G.L. Nesom, **comb. nov.** *Mimulus dentilobus* B.L. Rob. & Fernald, Proc. Amer. Acad. Arts 30: 120. 1894.
35. **Erythranthe glabrata** (Kunth) G.L. Nesom, **comb. nov.** *Mimulus glabratus* Kunth, Nov. Gen. Sp. (quarto ed.) 2: 370. 1817. Authorship of *M. glabratus* sometimes is attributed incorrectly to A. Gray.
36. **Erythranthe madrensis** (Seem.) G.L. Nesom, **comb. nov.** *Mimulus madrensis* Seem., Bot. Voy. Herald 9: 322, plate 58. 1856.
    Mimulus wiensii R.K. Vickery, Madroño 22: 161. 1973.

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37. **Erythranthe pallens** (Greene) G.L. Nesom, **comb. nov.** *Mimulus pallens* Greene, Leafl. Bot. Observ. Crit. 2: 4. 1909.
38. **Erythranthe pennellii** (Gentry) G.L. Nesom, **comb. nov.** *Mimulus pennellii* Gentry, Madroño 9: 24. 1947.
39. **Erythranthe visibilis** G.L. Nesom, Phytoneuron 2012-40: 97. 2012.

(SOUTH AMERICA-Chile)

40. **Erythranthe andicola** (Kunth) G.L. Nesom, **comb. nov.** *Mimulus andicola* Kunth, Nov. Gen. Sp. (quarto ed.) 2: 370. 1817 [publ. 1818].
41. **Erythranthe cuprea** (Dombrain) G.L. Nesom, **comb. nov.** *Mimulus cupreus* Dombrain, Fl. Mag. (London) 2: t. 70. 1862.
42. **Erythranthe depressa** (Phil.) G.L. Nesom, **comb. nov.** *Mimulus depressus* Phil., Fl. Atacam., 45. 1860.
43. **Erythranthe lacerata** (Pennell) G.L. Nesom, **comb. nov.** *Mimulus laceratus* Pennell, Physis (Buenos Aires) 9: 320. 1929.
44. **Erythranthe lutea** (L.) G.L. Nesom, **comb. nov.** *Mimulus luteus* L., Sp. Pl. (ed. 2), 884. 1763. Included as synonyms are *M. nummularis* Gay, *M. smithii* Lindl., and others).

    Erythranthe lutea var. **variegata** (Lodd.) G.L. Nesom, **comb. nov.** *Mimulus variegatus* Lodd., Bot. Cab. 16: t. 1872. 1832. *Mimulus luteus var. variegatus* (Lodd.) Hook. in Curtis, Bot. Mag. 61: tab. 3336. 1834.
45. **Erythranthe acaulis** (Phil.) G.L. Nesom, **comb. nov.** *Mimulus acaulis* Phil., Anales Univ. Chile 91: 112. 1895. *Mimulus depressus* var. *acaulis* (Phil.) Reiche, Fl. Chile 6: 62. 1911.

    Mimulus nanus Phil., Fl. Atacam., 45. 1860 (not *M. nanus* Hook. & Arn. 1839). *Mimulus depressus* var. *nanus* (Phil.) Reiche, Fl. Chile 6: 62. 1911.

    Mimulus minimus C. von Bohlen, Gayana, Bot. 52: 13. 1995.
46. **Erythranthe naiandina** (J.M. Watson & C. von Bohlen) G.L. Nesom, **comb. nov.** *Mimulus naiandinus* J.M. Watson & C. von Bohlen, Curtis's Bot. Mag. 17: 199. 2000.
47. **Erythranthe parviflora** (Lindl.) G.L. Nesom, **comb. nov.** *Mimulus parviflorus* Lindl., Bot. Reg. 11: , pl. 874. 1825 [not *Mimulus parviflorus* (Greene) A.L. Grant 1925 ("1924")].
48. **Erythranthe pilosiuscula** (Kunth) G.L. Nesom, **comb. nov.** *Mimulus pilosiusculus* Kunth, Nov. Gen. Sp. (quarto ed.) 2: 370. 1817 [publ. 1818].

Erythranthe glabrata sensu lato includes various South American taxa that may prove to be discrete biological entities, e.g., *Mimulus kingii* Phil., *M. sylvaticus* Phil., *M. tener* Phil., and others). In the sense adopted here and in a study of the section (Nesom 2012a), typical *E. glabrata* (typified by a Mexican plant) is known in South America only from a population system in Colombia.

Erythranthe lutea var. *lutea* has yellow corollas like those of western North America, while *E. lutea* var. *variegata* has purplish corolla lobes with a white to pale-yellow throat. *Erythranthe naiandina* has a purplish-pink corollas white on the distal half of the lower three lobes. *Erythranthe cuprea* has two color forms: orange-red and yellow (Cooley et al. 2008).

A detailed study of sect. *Simiola* (Nesom 2012a), published simultaneously with the present manuscript, includes maps, typifications, complete synonymy, descriptions, and a key to the species.

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APPENDIX: HOMOTYPIC SYNONYMY AND TAXONOMIC USAGE

I. MIMULUS L., Sp. Pl. Sp. 2: 634. 1753; L., Gen. Pl. 283. 1754; Benth., Scroph. Indicae 29 (1835), partly (as to *M. ringens*, *M. alatus*, *M. strictus*, *M. orbicularis*, *M. gracilis*); Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 405. 2004, partly; and other authors below. **TYPE**: *Mimulus ringens* L. The genus as originally described by Linnaeus included only a single species.

Monavia Adans., Fam. Plant. 2: 211. 1763, nom. illeg. (superfluous name: ICN Art. 52.1). Superfluous when published, intended by Adanson as a replacement name for *Mimulus* L., which was listed as a synonym. Not *Mimulus* of Plinius, which was treated by Adanson as the name for *Rhinanthus* of Linnaeus. **TYPE**: *Mimulus ringens* L.

Cynorrhynchium J. Mitchell, Diss. Brevis. Princ. Bot. Zool. 29. 1769, nom. illeg. (includes type of an existing genus: ICN Art. 52.1). **TYPE**: *Mimulus ringens* L. The 1769 protologue "exactly repeated Mitchell's previous description in Acta Phys.-Med. Acad. Caes. Leop.-Francisc. Nat. Cur. 8: 207. 1748; only the genus was described, but by Linnaeus' reference in the Genera Plantarum [1754 (ed. 5), p. 283] to *Cynorrhynchium* as a synonym of *Mimulus*, Mitchell's plant was correctly identified with *M. ringens* L." (Pennell 1935, p. 112). The description by Linnaeus also incorporated much of the original by Mitchell.

Most of Mitchell's herbarium and types are in BM-Banks, with others in G, LINN, and OXF but a collection of *Mimulus* by Mitchell apparently is not among them.

Mimulus § *Erecti* Benth. in DC., Prodr. 10: 369. 1846, without indication of rank, partly (as to *M. ringens*, *M. alatus*, *M. madagascariensis*, *M. gracilis*. **LECTOTYPE**: *Mimulus ringens* L. Bentham included *M. ringens*, *M. alatus*, *M. madagascariensis*, *M. gracilis*, *M. pusillus*, and *M. uvedaliae* in ser. *Erecti*. There is no clear choice for lectotype; the species selected.here is one that Bentham had studied from adequate material.

Mimulus § *Prostrati* Benth. in DC., Prodr. 10: 373. 1846, without clear indication of rank, partly (as to *M. orbicularis*). **LECTOTYPE**: *Mimulus orbicularis* Wall. ex Benth. Bentham included *M. orbicularis*, *M. repens*, and *M. prostratus*. He noted that these comprised "Species Asiaticæ vel Australasicæ." This section has not been adopted subsequently and in global works these species have been consistently treated together. There is no clear choice for lectotype; the species selected here is one that Bentham had studied from adequate material.

Mimulus subg. *Synplacus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126, partly.

Mimulus subg. *Synplacus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"). **LECTOTYPE**: *Mimulus ringens L.* Grant did not specify a type from among the four sections she included in subg. *Synplacus*. Typification of subg. *Synplacus* has not subsequently been made explicit and the subgenus has not been used to the exclusion of any sections or species among those with axile placentation. What species Grant may have had in mind as the type of subg. *Synplacus* is not clear — the choice here simply places the taxon as a synonym of *Mimulus* sensu stricto.

Mimulus § *Mimulus* (as "*Eumimulus*"): A. Gray, Proc. Amer. Acad. 11: 97 1876, partly,(as to *M. ringens* and *M. alatus*); Greene, Bull. Calif. Acad. Sci. 1: 108. 1885, partly (as to *M. ringens* and *M. alatus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 276. 1886, partly, 2(1): 446. 1886, partly (idem). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*"): Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876), partly; Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. gracilis*, *M. madagascariensis*); A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (to spp. listed under our sect. "*Eumimulus*" except *M. linearis*).

Mimulus sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. orbicularis*).

II. THYRIDIA W.R. Barker & Beardsley, **in text above.** **TYPE:** *Thyridia repens* (R. Br.) W.R. Barker & Beardsley.

Mimulus § *Prostrati* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, name without rank, partly (as to *M. repens*).

Mimulus sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876), partly.

Mimulus subg. *Synplacus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126, partly,

Mimulus sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. repens*).

Mimulus auct. non L. (partly, as to *M. repens*): Benth., Scroph. Indicae 29 (1835); Wettst., Nat. Pfl. IV 3b: 72 (1891); ?Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 405. 2004.

III. MICROCARPAEA R. Br., Prodr. Fl. Nov. Holland., 435. 1810; Benth. in DC., Prodr. 10: 432. 1846; Benth. & J.D. Hook., Gen. Pl. 2(2): 957 (1876); Wettst., Nat. Pfl. IV 3b: 77 (1891) ; Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 402. 2004. **TYPE:** *Microcarpaea muscosa* R. Br., nom. illeg. (= *Microcarpaea minima* (K.D. Koenig ex Retz.) Merrill), the only species in the protologue.

IV. UVEDALIA R. Br., Prodr. Fl. Nov. Holland., 440. 1810; Benth., Scroph. Indicae 8 (1835). **TYPE:** *Uvedalia linearis* R. Br., the only species in the protologue.

Mimulus § *Erecti* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, name without rank, partly (as to *M. uvedaliae*),

Mimulus subg. *Synplacus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126, partly. (as to *M. linearis.*).

Mimulus § *Mimulus* (as "*Eumimulus*") [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. 11: 97. 1876, partly, (as to *M. linearis*). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876), partly; Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. linearis* (R. Br.) Wettst.); A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (as to *M. linearis* and its var. *lutea*).

Mimulus auctt. non L., partly: authors since R. Br., Benth. (1835), and D. Don.

V. PEPLIDIUM Delile, Fl. Egypte [Edn. 1]: 148. 1813; [Delile, Descr. Egypte, Hist. Nat. 50, 148. 1813 ("1812"), nomen nudum]; Benth. in DC., Prodr. 10: 422. 1846; Benth. & J.D. Hook., Gen. Pl. 2(2): 957 (1876); Wettst., Nat. Pfl. IV 3b: 77. 1891; Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 402. 2004. **TYPE:** *Peplidium humifusum* Delile (= *Peplidium maritimum* (L.f.) Asch.), the only species in the protologue.

VI. ELACHOLOMA F. Muell. & Tate ex F. Muell., Vict. Naturalist 12: 14. May 1895 ("genus of Sesameae"); F. Muell. & Tate ex Tate, Trans. Roy. Soc. S. Austral. 19: 79. July 1895, nomen nudum ("Or. Pedalineae"); S.T. Blake, Proc. Roy. Soc. Queensl. 70: 45. 1959 (Scrophulariaceae); N.T. Burb., Dict. Austral. Pl. Gen. (Pedaliaceae or Scrophulariaceae); W.R. Barker, Fl. Cent. Austral. 329. 1981 (Scrophulariaceae); W.R. Barker, Evol. Fl. Fauna Arid Austral. 342. 1982 (Scrophulariaceae trib. Gratioleae subtrib. Mimulinae); Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 402. 2004 (Scrophulariaceae "Phrymaceae" trib. Microcarpaeeae (as "Microcarpeae"). **TYPE:** *Elacholoma hornii* F. Muell. & Tate, the only species in the protologue.

Mimulus § *Prostrati* auct. non Benth.: Benth. in DC., Prodr. 10: 373. 1846, without clear indication of rank, partly (excl. *M. orbicularis*, *M. repens*).

Mimulus § *Erecti* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, name without rank, partly (as to *M. pusillus*),

Mimulus sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: ?Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876), partly (as to Benth. in DC. citation).
Mimulus subg. *Synplacus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 126, partly (as to *M. prostratus*).
Mimulus sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. prostratus* and *M. pusillus*).
Mimulus auctt. non L.(partly, as to *M. prostratus* and/or *M. pusillus*): e.g. Benth., Fl. Austral. 4: 483. 1868; W.R. Barker, Fl. Cent. Austral. 329. 1981

VII. GLOSSOSTIGMA Wight & Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 355. 1836, nom. conserv.; Benth. in DC., Prodr. 10: 426. 1846; Benth. & J.D. Hook., Gen. Pl. 2(2): 958 (1876); Wettst., Nat. Pfl. IV 3b: 78. 1891; Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 403. 2004. **TYPE**: *Glossostigma spathulatum* Arn., nom. illeg. (*Limosella diandra* L. = *Glossostigma diandrum* (L.) Kuntze), the only species in the protologue.
Tricholoma Benth. in DC., Prodr. 10: 426. 1846, nom. rejic. **TYPE**: *T. elatinoides* Benth. = *G. elatinoides* (Benth.) Benth. ex J.D. Hook., non *Tricholoma* (Fr.) Staude, nom. cons. (Fungi: Agaricaceae), the sole species in the protologue.
Mimulus sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Benth. & J.D. Hook., Gen. Pl. 2(2): 958 (1876), partly.

VIII. PHRYMA L., Sp. Pl. 2: 601. 1753; Schauer in DC. Prod. 11: 520. 1847 (in monotypic Phrymaceae); Benth. & J.D. Hook., Gen. Pl. 2(2): 1132 (1876) (as Verbenaceae trib. Phrymeae); Briq., Nat. Pfl. IV 3b: 361 (in monotypic Phrymaceae). 1891; Thieret, J. Arnold Arb. 53: 226. 1972; Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 402. 2004 (in Scrophulariaceae "Phrymaceae", in note only). **TYPE**: *Phryma leptostachya* L., the sole species in the protologue.
Leptostachia Adans., Fam. 2: 201. 1763. A superfluous replacement name for *Phryma* L.

IX. HEMICHAENA Benth., Pl. Hartw., 78. 1841; Benth. & J.D. Hook., Gen. Pl. 2(2): 943 (1876); Wettst., Nat. Pfl. IV 3b: 67. 1891; Thieret, Fieldiana Bot. 34: 92. 1972; Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 404. 2004. **TYPE**: *Hemichaena fruticosa* Benth. (= *Mimulus fruticosus*).
Mimulus (subg. *Schizoplacus*) sect. *Tropanthus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 324. 1925 ("1924"). **TYPE**: *Mimulus treleasei* A.L. Grant (= *Mimulus levigatus*). This is the sole species in the protologue.
Berendtia A. Gray, Proc. Amer. Acad. Arts 7: 379. 1868 (non Goeppert 1845); Wettst., Nat. Pfl. IV 3b: 67. 1891; A.L. Grant, Ann. Missouri Bot. Gard. 11: 350. 1925 ("1924") (in note). — *Berendtiella* Wettst. & Harms in Engl. et Prantl, I Pflanzenf., Gesamtregister zum II. bis IV. Teil: 459. 1899 [a replacement name for *Berendtia* A. Gray]. **LECTOTYPE** (Thieret 1972b, p. 92): *Berendtia ghiesbrechtii* A. Gray (= *Mimulus rugosus*). Gray did not cite a type for his new genus, in which he included *B. ghiesbrechtii*, *B. coulteri*, and *B. rugosa*.
Leucocarpus auct. non D. Don: Benth in DC., Prodr. 10: 335. 1846, partly (as to *L. fruticosus*).
Diplacus auct. non Nutt.: Benth in DC., Prodr. 10: 335. 1846, partly (as to *D. rugosus*). — *Mimulus* sect. *Diplacus* auct. non (Nutt.) Wettst.: Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. rugosus*).

X. MIMETANTHE Greene, Bull. Calif. Acad. Sci. 1: 181. 1886[1885]; A.L. Grant, Ann. Missouri Bot. Gard. 11: 350. 1925 ("1924"); Wettst., Nat. Pfl. IV 3b: 67. 1891 (as "*Mimelanthe*"; A.L. Grant, Ann. Missouri Bot. Gard. 11: 350. 1925 ("1924") (in note). Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 405. 2004. **TYPE**: *Mimetanthe pilosa* (Benth.) Greene
Herpestis sect. *Mimuloides* Benth. in DC., Prodr. 10: 394. 1846. — *Mimulus* § *Mimuloides* (Benth.) Benth. & J.D. Hook., Gen. Pl. 2(2): 947. 1876; A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876; Greene, Bull. Calif. Acad. Sci. 1: 122. 1885; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2:

279. 1886; 2(1): 446. 1886. **TYPE**: *Herpestis pilosa* Benth. [=*Mimetanthe pilosa*] Watson (1871) noted that the species had been recognized as *Herpestis* sect. *Mimuloides* but he did not formally transfer the section to *Mimulus*.

XI. DIPLACUS Nutt., Ann. Nat. Hist. 1: 137. 1838; Benth. in DC., Prodr. 10: 368. 1848, partly (excl. *D. rugosus*); Greene, Bull. Calif. Acad. Sci. 1: 94. 1885. — *Mimulus* § *Diplacus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876 (as to spp. in our sect. *Diplacus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 275. 1886 (as to spp. listed under our sect. *Diplacus*), 2(1): 442. 1886. — *Mimulus* sect. *Diplacus* (Nutt.) Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876); Wettst., Nat. Pfl. IV 3b: 71 (1891), partly (as to spp. listed under our sect. *Diplacus*). — *Mimulus* (subg. *Schizoplacus*) sect. *Diplacus* (Nutt.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 326. 1925 ("1924") (as to spp. in our sect. *Diplacus*). **LECTOTYPE** (Thompson 2005): *Diplacus glutinosus* (J.C.Wendl.) Nutt. [= *Diplacus aurantiacus*]

Eunanus Benth. in DC., Prodr. 10: 374. 1846; Greene, Bull. Calif. Acad. Sci. 1: 94. 1885, partly. — *Mimulus* § *Eunanus* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876 (as to spp. in our sects. *Erimimimulus*, *Eunanus*, *Oenoe*, *Cleisanthus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 273. 1886 (as to spp. listed under our sects. *Erimimimulus*, *Eunanus*, *Oenoe*, *Cleisanthus*), 2(1): 444. 1886 (as to spp. listed under our sects. *Erimimimulus*, *Eunanus*, *Cleisanthus*). — *Mimulus* sect. *Eunanus* (Benth.) Wettst.: Wettst., Nat. Pfl. IV 3b: 71 (1891) (no spp. listed). — *Mimulus* (subg. *Schizoplacus*) sect. *Eunanus* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924") (as to spp. listed under our sects. *Erimimimulus*, *Eunanus*, *Pseudoenoe*, *Cleisanthus*). **LECTOTYPE** (see under *Diplacus* sect. *Eunanus*).

Mimulus subg. *Schizoplacus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924"). **LECTOTYPE**: (Thompson 2005, p. 26): *Mimulus nanus* Hook. & Arn.[= *Diplacus nanus*]

Mimulus § *Oenoe* A. Gray in W.H. Brewer, S. Watson, and A. Gray, Bot. California (ed. 1): 563. 1876; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 443. 1886 (as to spp. listed under our sects. *Oenoe*, *Cleisanthus*). — *Eunanus* sect. *Oenoe* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. angustatus*, *E. tricolor*). — *Mimulus* sect. *Oenoe* (A. Gray) Wettst., Nat. Pfl. IV 3b: 71 (1891) (no spp. listed). — *Mimulus* sect. *Oenoe* (A. Gray.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 309. 1925 ("1924"), partly (as to spp. listed under our sects. *Oenoe*, *Cleisanthus*). **TYPIFICATION** (see under sect. *Oenoe*).

Mimulus § *Mimulastrum* A. Gray in Lemmon, Bot. Gaz. (Crawfordsville) 9: 141. 1884; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 446. 1886, partly (as to *M. mohavensis*). — *Eunanus* § *Mimulastrum* (A. Gray) Greene, Bull. Calif. Acad. Sci. 1: 105. 1885 (as to *M. pictus*, *M. mohavensis*). — *Mimulus* sect. *Mimulastrum* (A. Gray) Wettst., Nat. Pfl. IV 3b: 71 (1891). — *Mimulus* sect. *Mimulastrum* (A. Gray) A.L. Grant, Ann. Missouri Bot. Gard. 11: 308. 1925 ("1924") (as to spp. listed under our sect. *Eunanus*). **TYPIFICATION** (see under sect. *Mimulastrum*).

Mimulus sect. *Pseudoenoe* A.L. Grant, Ann. Missouri Bot. Gard. 11: 323. 1925 ("1924") (as to our sect. *Pseudoenoe*). **TYPIFICATION** (see under sect. *Pseudoenoe*).

Mimulus § *Speciosi* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, partly (as to *M. brevipes*).

Mimulus auct. non L.: Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 405 2004, partly.

1. DIPLACUS sect. **EREMIMIMULUS** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Diplacus parryi* (A. Gray) G.L. Nesom & N.S. Fraga

Mimulus (subg. *Schizoplacus*) sect. *Eunanus* auct. non (Benth.) A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (as to *M. parryi*).

Eunanus sect. *Eunanus* [auct. non Greene]: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. parryi*). — *Mimulus* § *Eunanus* auct. non (Benth.) A. Gray: A. Gray, Proc. Amer. Acad. 11: 97 1876, partly (as to *M. parryi*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 445. 1886, partly (as to *M. parryi*).

2. DIPLACUS sect. **EUNANUS** (Benth.) G.L. Nesom & N.S. Fraga, **in text above.** *Eunanus* Benth. in DC., Prodr. 10: 374. 1846 , partly (as to *E. fremontii*, *E. tolmiei*). — *Mimulus* § *Eunanus* (Benth.) A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. leptaleus*¸*M. bigelovii*, *M. nanus*, *M., fremontii*, *M. bolanderi*, *M. brevipes*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 444. 1886 (as to *M.bigelovii*, *M. bolanderi*, *M brevipes*, *E. fremontii*, *E. leptaleus*, *M. mephiticus*, *M. nanus*, *M. rattanii*, *M. whitneyi*). — *Eunanus* sect. *Eunanus*: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. leptaleus*, *E. bigelovii*, *E. mephiticus*, *E. tolmiaei*, *E. fremontii*, *E. layneae*, *E. torreyi*, *E. rattanii*, *E. bolanderi*, *E. brevipes*). — *Mimulus* sect. *Eunanus* (Benth.) Wettst., Nat. Pfl. IV 3b: 71 (1891). — *Mimulus* (subg. *Schizoplacus*) sect. *Eunamus* (Benth.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924"), partly (as to *M. brevipes*, *M. spissus, M. bigelovii*, *M. johnstonii*, *M. cusickii*, *M. fremontii*, *M. subsecundus* and vars., *M. decurtatus*, *M. rattanii*, *M. layneae*, *M. nanus*, *M. clivicola*, *M. angustifolius*, *M. mephiticus*, *M. leptaleus*, *M. jepsonii*, *M. whitneyi*) **LECTOTYPE** (Thompson 2005): *Eunanus tolmiei* Benth. [= *Diplacus nanus* (Hook. & Arn.) G.L. Nesom & N.S. Fraga]

Mimulus § *Mimulastrum* A. Gray in Lemmon, Bot. Gaz. (Crawfordsville) 9: 141. 1884, partly (as to *M. mohavensis*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 446. 1886, partly (idem). — *Eunanus* § *Mimulastrum* (A. Gray) Greene, Bull. Calif. Acad. Sci. 1: 105. 1885, partly (idem). — *Mimulus* sect. *Mimulastrum* (A. Gray) Wettst., Nat. Pfl. IV 3b: 71 (1891), partly (idem). — *Mimulus* (subg. *Schizoplacus*) sect. *Mimulastrum* (A. Gray) A.L. Grant, Ann. Missouri Bot. Gard. 11: 308. 1925 ("1924"). **TYPE:** *Mimulus mohavensis* Lemmon. Gray (in Lemmon) included only *M. mohavensis* in the new section. See comments below under sect. *Pseudonoe*.

Mimulus § *Speciosi* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, partly (as to *M. brevipes*).

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. brevipes*).

3. DIPLACUS sect. **PSEUDOENOE** (A.L. Grant) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* sect. *Pseudoenoe* A.L. Grant, Ann. Missouri Bot. Gard. 11: 323. 1925 ["1924"]. **TYPE:** *Mimulus pictus* (Curran ex Greene) A. Gray [= *Diplacus pictus*]. Gray (in Lemmon 1884) included only *M. mohavensis* in sect. *Mimulastrum* but Greene (1885) added *M. pictus* (as *Eunanus pictus*) to the section, and Gray (1886) also included both species in sect. *Mimulastrum.* With Grant's (1924) creation of sect. *Pseudoenoe* for *M. pictus*, each species thus constituted a monotypic section in her treatment.

Mimulus § *Mimulastrum* auct. non A. Gray (partly, as to *M. pictus*, see note below): Greene, Bull. Calif. Acad. Sci. 1: 105. 1885; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 446. 1886. — *Mimulus* sect. *Mimulastrum* auct. non (A. Gray) Wettst.: Wettst., Nat. Pfl. IV 3b: 71 (1891), partly (as to *M. pictus*);

4. DIPLACUS sect. **OENOE (**A. Gray) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* § *Oenoe* A. Gray in W.H.Brewer, S.Watson, and A. Gray, Bot. California (ed. 1): 563. 1876; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 445. 1886, partly (as to *M. angustatus*, *M. tricolor*). — [*Oenoe* A. Gray in Benth., Pl. Hartw. 329. 1849, nom. inval. (under *Eunanus douglasii*, Bentham appears to suggest that, instead of within *Eunanus*, the species would be better considered within Gray's genus *Oenoe*, but in 1849 the name *Oenoe* apparently had not yet been published at any rank] — *Eunanus* sect. *Oenoe* (A. Gray) Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. angustatus*, *E. tricolor*). — *Mimulus* sect. *Oenoe* (A. Gray) Wettst., Nat. Pfl. IV 3b: 71 (1891). — *Mimulus* (subg. *Schizoplacus*) sect. *Oenoe* (A. Gray.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 309. 1925 ("1924"), partly (as to *M. pygmaeus*, *M. tricolor*, *M. angustatus*. **LECTOTYPE** (Thompson 2005): *Mimulus tricolor* Hartweg ex Lindley [= *Diplacus tricolor*]

Mimulus sect. *Microphyton* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 170. 1947. **TYPE**: *Mimulus pygmaeus* A.L. Grant, the only species included in the protologue.

Mimulus § *Eunanus* auct. non (Benth.) A. Gray: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. tricolor* and its *var. angustatus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 274. 1886, partly (as to *M. angustatus*, *M. tricolor*).

5. DIPLACUS sect. DIPLACUS

Mimulus § *Diplacus* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 11: 97. 1876; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 275. 1886, 2(1): 442. 1886. — *Diplacus* Nutt., Ann. Nat. Hist. 1: 137. 1838; Benth. in DC., Prodr. 10: 368. 1846, partly (as to *D. glutinosus*, *D. leptanthus*, *D. longiflorus*). — *Mimulus* sect. *Diplacus* (Nutt.) Wettst., Nat. Pfl. IV 3b: 71 (1891), partly (as to *M. glutinosus*, *M. puniceus*). — *Mimulus* (subg. *Schizoplacus*) sect. *Diplacus* (Nutt.) A.L. Grant, Ann. Missouri Bot. Gard. 11: 326. 1925 ("1924") (as to *M. clevelandii*, *M. longiflorus* and vars. *calycinus* and *linearis*, *M. leptanthus*, *M. aridus*, *M. stellatus*, *M. aurantiacus*, *M. puniceus*, *M. parviflorus*). **LECTOTYPE** (Thompson 2005): *Diplacus glutinosus* (J.C.Wendl.) Nutt. [= *Diplacus aurantiacus*]

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. linearis*, *M. glutinosis*)

6. DIPLACUS sect. CLEISANTHUS (J.T. Howell) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* sect. *Cleisanthus* J.T. Howell, Leafl. W. Bot. 2: 80. 1938. **TYPE**: *Mimulus cleistogamus* J.T.Howell [= *Diplacus douglasii*]. The original circumscription of the section included only *M. cleistogamus*.

Eunanus Benth. in DC., Prodr. 10: 374. 1846, partly (as to *E. douglasii*). — *Mimulus* § *Eunanus* auct. non (Benth.) A. Gray: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. torreyi*, *M. douglasii* and *M. latifolius*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 274. 1886 (as to *M. douglasii*, *M. kelloggii*, *M. latifolius*, *M. torreyi*), 2(1): 443. 1886, partly (as to *M. torreyi*). — *Mimulus* (subg. *Schizoplacus*) sect. *Eunanus* auct. non (Benth.) A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924"), partly (as to *M. torreyi*). — *Eunanus* sect. *Eunanus* [auct. non Greene]: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. kelloggii*, *E. torreyi*).

Eunanus sect. *Oenoe* auct. non (A. Gray.) Greene: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. douglasii*, *E. latifolius*). — *Eunanus* § *Oenoe* auct. non A. Gray: A, Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 443. 1886, partly (as to *M. douglasii*, *M. kelloggii*, *M. latifolius*). — *Mimulus* (subg. *Schizoplacus*) sect. *Oenoe* auct. non (A. Gray) A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 268. 1925 ("1924"), partly (as to *M. latifolius*, *M. congdonii*, *M. kelloggii*, *M. douglasii*, *M. traskiae*).

XII. LEUCOCARPUS D.Don in Sweet, Brit. Flower Gard. ser. 2, 2: pl. 124. 1831; Benth. in DC., Prodr. 10: 335. 1846, partly (excl. *L. fruticosus*); Benth. & J.D. Hook., Gen. Pl. 2(2): 943 (1876); Wettst., Nat. Pfl. IV 3b: 63 (1891); A.L. Grant, Ann. Missouri Bot. Gard. 11: 350. 1925 ("1924") (in note); Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 404. 2004. — *Mimulus* sect. *Leucocarpus* (D.Don) G.L. Nesom, Phytoneuron 2011-36: 4. 2011. **TYPE**: *Leucocarpus alatus* (Graham) Benth. [= *Leucocarpus perfoliatus*]

XIII. ERYTHRANTHE Spach, Hist. Nat. Veg. Phan. 9: 312. 1838 ["1840"]. — *Mimulus* §. *Erythranthe* (Spach) Greene, Bull. Calif. Acad. Sci. 1: 108. 1885. — *Mimulus* (subg. *Synplacus*) sect. *Erythranthe* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 137. 1925 ("1924) (as to ssp. in our sect. *Erythranthe*). **TYPE**: *Erythranthe cardinalis* (Douglas ex Benth.) Spach, the only species in the protologue.

Mimulus (subg. *Synplacus*) sect. *Paradanthus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (see spp. listed under our sects. except *Semigemma*, *Simiola*). TYPE (see under sect. *Paradantha*)

Eunanus Benth. sect. *Eunanus* [auct. non Greene]: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to species in sect. *Monimanthe*).

Mimulus § *Simiolus* Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to spp. in all sects. bar *Erythranthe*, *Sinopitheca*). — *Mimulus* (subg. *Synplacus*) sect. *Simiolus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924") (as to spp. listed under our sects. *Mimulosma*, *Simiola*). TYPE (see under sect. *Simiola*)

Mimulus § *Speciosi* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, partly (as to spp. listed under our sects. *Monanthe*, *Erythranthe*, *Simiola*)

Mimulus § *Teneri* auct. non Benth.: Benth. in DC., Prodr. 10: 372. 1846, partly (as to spp. listed under our sects. *Alsinimimulus*, *Mimulosma*, *Mimulasia*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to spp. listed under our sect. *Achlyopitheca*, *Paradantha*, *Monantha*, *Erythrantha*, *Alsinimimula*, *Mimulosma*, *Mimulasia*, *Simiola*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 276. 1886, partly (as to spp. in all sections but *Mimulasia*, *Sinopitheca*, *Exigua*), 2(1): 446. 1886, partly (as to spp. in all sections but *Mimulasia*, *Sinopitheca*). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*") [auct .non Benth. & J.D. Hook.]: Benth. & J.D. Hook., Gen. Pl. 2(2): 947 (1876), partly; Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to spp. listed under our sects. *Mimulosma*, *Mimulasia*, *Simiola*).

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to species listed under our sects. *Erythranthe*, *Simiola*, *Mimulosma*, *Alsinimimula*, *Monantha*, *Mimulasia*); Benth. in DC., Prodr. 10: 368. 1846, partly; Greene, Bull. Calif. Acad. Sci 1: 98. 1885, partly (see under sect. *Simiola*); Eb. Fisch., Fam. Gen. Vasc. Pl. 7: 405. 2004, partly.

1. **ERYTHRANTHE** sect. **ACHLYOPITHECA** N.S. Fraga & G.L. Nesom, **in text above.** **TYPE**: *Erythranthe inconspicua* (A. Gray) G.L. Nesom & N.S. Fraga

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. inconspicuus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 276. 1886, partly (as to *M. inconspicuus*), 2(1): 449. 1886, partly (as to *M. inconspicuus* and its var. *acutidens*).

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. inconspicua*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (as to *M. acutidens* Greene, *M. grayi*, *M. inconspicuus*, *M. acutidens*,).

2. **ERYTHRANTHE** sect. **PARADANTHA** (A.L. Grant) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* (subg. *Synplacus*) sect. *Paradanthus* A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. palmeri*, *M. gracilipes*,*M. androsaceus*, *M. diffusus*, *M. purpureus*, *M. discolor*, *M. montioides*, *M. deflexus* , *M. suksdorfii*, *M. rubellus*,). **LECTOTYPE**: *Mimulus rubellus* A. Gray [= *Erythranthe rubella*]. Grant specified only that sect. *Paradanthus* comprised "Sp. 26–69" but observed that "*M. rubellus* is at the center of the section" and is closely allied with members of the *Mimulus palmeri* group.

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. rubellus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 278. 1886, partly (as to *M. montioides*, *M. palmeri*, *M. rubellus*), 2(1): 450. 1886, partly (also as to *M. suksdorfii*).

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. montioides*, *M. rubellus*, *M. palmeri*, *M. androsaceus*).

3. ERYTHRANTHE sect. **MONANTHA** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe primuloides* (Benth.) G.L. Nesom & N.S. Fraga

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. primuloides*).

Mimulus § *Speciosi* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, partly (as to *M. primuloides*)

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. primuloides*): A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 278. 1886, partly (as to *M. primuloides*), 2(1): 450. 1886, partly (also as to *M. linearifolia*)

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. primuloides*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. primuloides*).

4. ERYTHRANTHE sect. **MONIMANTHE** (Pennell) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* sect. *Monimanthe* Pennell, Proc. Acad. Nat. Sci. Philadelphia 99: 167. 1947. **TYPE**: *Mimulus breweri* (Greene) Coville [= *Erythranthe breweri*]

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. bicolor*, *M. bioletii*, *M. filicaulis*, *M. breweri*).

Eunanus sect. *Eunanus* [auct. non Greene]: Greene: Greene, Bull. Calif. Acad. Sci 1: 98. 1885 (rank specified on p. 97), partly (as to *E. breweri*, *E. bicolor*).

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. bicolor*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray] (partly, as to *M. bicolor*): A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 278. 1886, 2(1): 450. 1886.

5. ERYTHRANTHE sect. **ERYTHRANTHE**

Mimulus § *Erythranthe* (Spach) Greene, Bull. Calif. Acad. Sci. 1: 108. 1885 (as to *M. cardinalis, M. lewisii, M. parishii*) . — *Mimulus* (subg. *Synplacus*) sect. *Erythranthe* (Spach) A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924") (as to *M. cardinalis*, *M. rupestris*, *M. verbenaceus*, *M. nelsonii*). **TYPE** (see under genus).

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. lewisii*, *?M. roseus*, *M. cardinalis*).

Mimulus § *Speciosi* auct. non Benth.: Benth. in DC., Prodr. 10: 369. 1846, partly (as to *M. cardinalis*, *M. lewisii*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. cardinalis*, *M. lewisii*); Gray, Syn. Fl. N. Amer. (ed. 2) 2: 276. 1886, partly (as to *M. cardinalis*, *M. lewisii*), 2(1): 446. 1886, partly (as to *M. cardinalis*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 126. 1925 ("1924"), partly (as to *M. eastwoodiae, M. lewisii*, *M. parishii*).

6. ERYTHRANTHE sect. **ALSINIMIMULUS** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe alsinoides* (Douglas ex Benth.) G.L. Nesom & N.S. Fraga

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. alsinoides*)

Mimulus § *Teneri* auct. non Benth.: Benth. in DC., Prodr. 10: 372. 1846, partly (as to *M. alsinoides*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray] (partly, as to *M. alsinoides*): A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876; A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 277. 1886, 2(1): 449. 1886.

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. alsinoides*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924") partly (as to *M. alsinoides*).

8. ERYTHRANTHE sect. **MIMULOSMA** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe moschata* (Douglas ex Lindl.) G.L. Nesom & N.S. Fraga

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. moschatus*, *M. floribundus*, *M. peduncularis*).

Mimulus § *Teneri* auct. non Benth.: Benth. in DC., Prodr. 10: 372. 1846, partly (as to *M. floribundus*, *M. pubescens*, *M. moschatus*).

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. pulsiferae*, *M. floribunda*, *M. moschatus*, *M. inodorus*, *M. moniliformis*). — *Mimulus* (subg. *Synplacus*) sect. *Simiolus* auct. non (Greene) A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 145. 1925 ("1924"), partly (as to *M. crinitus*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. breviflorus*, *M. latidens*, *M. pulsiferae*, *M. washingtonensis*, *M. ampliatus*, *M. arenarius*, *M. floribundus*, *M. jungermannioides*, *M. moschatus*, *M. leibergii*, *M. dudleyi*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. pulsiferae*, *M. floribundus*, *M. moschatus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 277. 1886, partly (as to *M. floribundus*, *M. moschatus* and its var. *longiflorus*, *M. pulsiferae*) , 2(1): 446. 1886, partly (idem). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. moschatus*).

9. ERYTHRANTHE sect. **MIMULASIA** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe tenella* (Bunge) G.L. Nesom & N.S. Fraga

Mimulus § *Teneri* Benth. in DC., Prodr. 10: 372. 1846, partly (as to *M. tenellus*, *M. dentatus*, *M. nepalensis*). **LECTOTYPE**: *Mimulus tenellus* Bunge. In addition to *M. nepalensis*, *M. tenellus* and *M. dentatus*, Bentham also included *M. alsinoides*, *M. floribundus*, *M. pubescens*, *M. moschatus*, and *M. orizabae* in § *Teneri*. The last five species are placed here into three other sections, thus Bentham's group was polyphyletic. The choice of type must be from among *M. nepalensis*, *M. tenellus*, and *M. dentatus*, and because the position of *M. dentatus* is not unequivocal, an Asian species is chosen. As Bentham's group names as plural adjectives are not clearly ranked (see comments above), a new, substantive name is chosen for the group.

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. dentatus*). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. tenellus*, *M. nepalensis*)

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. dentatus*).

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. nepalensis, M. bridgesii*).

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. nepalensis*).

10. ERYTHRANTHE sect. **SINOPITHECA** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe sessilifolia* (Maxim.) G.L. Nesom & N.S. Fraga

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. sessilifolius*, *M. bridgesii*).

11. ERYTHRANTHE sect. **EXIGUA** G.L. Nesom & N.S. Fraga, **in text above. TYPE**: *Erythranthe exigua* (A. Gray) G.L. Nesom & N.S. Fraga

Mimulus (subg. *Synplacus*) sect. *Paradanthus* auct. non A.L. Grant: A.L. Grant, Ann. Missouri Bot. Gard. 11: 195. 1925 ("1924"), partly (as to *M. exiguus*).

Mimulus § *Simiolus* auct. non Greene: Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. exiguus*).

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 451. 1886, partly (as to *M. exiguus*).

12. ERYTHRANTHE sect. **SIMIOLA** (Greene) G.L. Nesom & N.S. Fraga, **in text above.** *Mimulus* § *Simiolus* Greene, Bull. Calif. Acad. Sci. 1: 109. 1885, partly (as to *M. tilingii*, *M. guttatus*, *M. microphyllus*, *M. nasutus*, *M. hallii*, *M. glaucescens*, *M. nudatus*, *M. laciniatus*, *M. jamesii*). — *Mimulus* (subg. *Synplacus*) sect. *Simiolus* (Greene) A.L. Grant, Ann. Missouri Bot. Gard. 11: 145. 1925 ("1924"), partly (excl. *M. crinitus*). **LECTOTYPE**: *Mimulus guttatus* Fisch. ex DC. [= *Erythranthe guttata*] *Mimulus guttatus* is chosen as the type because it often is considered the "central" species of the section, often regarded as inclusive of many of the other species or regarded as directly ancestral to them.

Mimulus § *Speciosi* Benth. in DC., Prodr. 10: 369. 1846, partly (as to *M. luteus*, *M. scouleri*, *M. glabratus*, *M. pilosiusculus*, *M. parviflorus*, *M. propinquus*, *M. jamesii*, *M. microphyllus*). **LECTOTYPE** (designated here): *Mimulus luteus L.* *Mimulus luteus* is chosen here as lectotype because it is the "showiest" of the species listed by Bentham, corresponding to his epithet "speciosi."

Mimulus § *Mimulus* (as *"Eumimulus"*) [auct. non A. Gray]: A. Gray, Proc. Amer. Acad. Arts 11: 95. 1876, partly (as to *M. luteus*, *M. jamesii*, *M. laciniatus*); A. Gray, Syn. Fl. N. Amer. (ed. 2) 2: 276. 1886, partly (as to *M. jamesii*, syn. *M. guttatus*, *M. laciniatus*, *M. luteus*, syn. *M. scouleri*), 2(1): 448. 1886, partly (also as to *M. glaucescens*, *M. nasutus*, *M. nudatus*). — *Mimulus* sect. *Mimulus* (as "*Eumimulus*") [auct. non Benth. & J.D. Hook.]: Wettst., Nat. Pfl. IV 3b: 72 (1891), partly (as to *M. parviflorus* Lindl., *M. luteus*).

Mimulus auct. non L.: Benth., Scroph. Indicae 29 (1835), partly (as to *M. luteus*, *M. lyratus*, *M. guttatus*, *M. parviflorus*, *M. glabratus*, *M. andicolus*, *M. pilosiusculus*).